INVASIVE REED CANARY GRASS (*PHALARIS ARUNDINACEA*) AND CARBON SEQUESTRATION IN A WETLAND COMPLEX

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To Mother and Father

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ABSTRACT

Jonathan S. Bills

INVASIVE REED CANARY GRASS (*PHALARIS ARUNDINACEA*) AND CARBON SEQUESTRATION IN A WETLAND COMPLEX

Terrestrial carbon sequestration is one of several proposed strategies to reduce the rate of carbon dioxide (CO_2) accumulation in the atmosphere, but the impact of plant invasion on soil organic carbon (SOC) storage is unclear. The results of past studies are often confounded by differences in vegetation and environmental conditions. Reed canary grass (*Phalaris arundinacea*) is an herbaceous species that invades riparian fringes and wetlands throughout North America, including Beanblossom Bottoms – a wetland complex in south-central Indiana. Because of the prolific growth of *P. arundinacea*, it was hypothesized that significant alterations in SOC pools and dynamics would occur at invaded sites within the wetland complex. To test this hypothesis, study plots were established in areas colonized either by native herbaceous species or by *P. arundinacea*. Above and below-ground biomass were collected at the middle and end of the growing season and were analyzed for cellulose, lignin, acid detergent fiber, total phenolics, and organic carbon and nitrogen concentration. Soil samples were analyzed for SOC and nitrogen, bulk density, pH, and texture. The biomass of *Scirpus cyperinus* – a native wetland species was found to contain significantly ($P < 0.05$) more lignin (168 g kg^{-1} versus 98 g kg^{-1}) and phenolics (19 g kg^{-1} versus 3 g kg^{-1}), and had a higher C to N ratio (28 versus 20) than

P. arundinacea biomass, suggesting greater recalcitrance of *S. cyperinus* tissues compared to *P. arundinacea* biomass. Results of a laboratory incubation study were consistent with the residue biochemistry data and showed that *S. cyperinus* biomass degraded at much slower rates than the biomass of *P. arundinacea*. However, measurements of SOC pools (0-30 cm) showed larger pools under *P. arundinacea* (25.5 Mg C ha^{-1}) than under stands of *S. cyperinus* (21.8 Mg C ha^{-1}). Likewise, SOC stocks under stands of mixed native vegetation were significantly ($P < 0.05$) smaller (18.8 Mg C ha^{-1}) than in areas invaded by *P. arundinacea*. Biomass of the mixed native vegetation was also considered more recalcitrant than that of *P. arundinacea* based on residue biochemistry. Therefore, contrary to the study hypothesis, residue quality was not a good predictor of SOC stocks in the wetland soils. Thus, it appears that traditional laboratory assessments of biomass recalcitrance and decomposition do not accurately simulate the various biological interactions occurring in the field.

Pierre-Andre Jacinthe, Ph.D., Committee Chair

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INTRODUCTION

Global Warming

Since the onset of the industrial revolution, the atmospheric CO_2 concentration has grown from 200 ppm to 380 ppm (IPCC, 2007). Combustion of fossil fuel and degradation of forest ecosystems are the main contributors to that increase. It is estimated that this increase in atmospheric CO_2 (1.3 - 9.45 ppm CO_2 yr^{-1}) could result in a 0.2 to 0.4 °C increase in global temperature per decade (IPCC, 2007).

Carbon Sequestration

Terrestrial carbon sequestration is one of several proposed approaches to reduce the rate of CO_2 accumulation in the atmosphere. It involves fixation of atmospheric CO_2 by vascular plants and the conversion of plant biomass into soil organic carbon fractions that persist for long periods. During photosynthesis, atmospheric CO_2 is converted into glucose and other biochemical molecules needed for the construction of plant biomass. When plants senesce and die, the biochemical products contained in plant tissues are introduced into the soil profile and undergo decomposition by soil microbes. These biochemical products vary in their resistance to microbial degradation. Simple molecules (e.g. glucose and amino acids) are degraded rapidly whereas more resistant biochemical molecules can persist in the soil profile for decades (Fog, 1988; Neff et al., 2002). It is expected that plant biomass containing recalcitrant bio-molecules (i.e. lignin and phenols) will result in larger pools of soil organic carbon (SOC) than biomass rich in simple carbohydrates. Ratios

of resistant/nonresistant biochemical molecules vary with plant species (Tian et al., 1995; Martens; 2000; Berg, 2000).

Biomass decomposition is related to the lignin and phenolic content of the plant material (Fog, 1988; Tian et al., 1995; Berg, 2000; Martens, 2000). It appears that the rate of lignin decomposition is regulated by other constituents of biomass; it increases when cellulose content is high and decreases when the nitrogen content of biomass is high (Fog, 1988; Berg, 2000). Berg (2000) emphasized that lignin is less critical in controlling decomposition in early stages of biomass degradation, but later takes a dominant role and significantly suppresses decomposition as holocellulose and other easily metabolizable carbohydrates are used up. Lignin degradation is carried out by "white-rot" basidiomycetes and other fungi of the *Imperfecti* group. Decomposition generally involves depolymerization of lignin, as a way of accessing cellulose and hemicellulose sheltered by the bonding structure of lignin (Paul and Clark, 1996; Berg, 2000). Phenols are another type of complex carbon structure that inhibits decomposition. Salusso (2000) demonstrated that wood species containing higher phenolic content resisted decay by *Pleurotus laciniatocrenatus*, a white rot fungus, better than other species less enriched in these substances.

Tian et al. (1995) developed an index of residue quality based on the C:N ratio, lignin, and polyphenol content of plants in the sub humid tropics. Their study was conducted with the goal of finding plant residues that decompose readily and release plant available nutrients in agroforestry systems. However, the index could also be used to evaluate the residues of wetland plants with the goal of identifying species producing recalcitrant biomass. The degradation products of these recalcitrant

residues could lead to the formation of stable soil organic carbon through humification.

Tan et al. (2004) noted that poor soil drainage and heavy texture favored soil carbon sequestration regardless of land use. They also showed that individual site variables effect soil carbon sequestration in the following manner:

soil order>drainage>texture>>slope>elevation.

Therefore, controlling for soil type and hydrology is critical in studies that seek to determine the effect of different plant species on carbon sequestration.

Carbon Stabilization Pathways

Other than the oceans, soils represent the largest carbon store in the biosphere, even larger than terrestrial plants (Schlesinger, 1997; Fig. 1). Paul et al. (2001) described soil organic carbon as "a complex mixture of materials that includes plant residues with known constituents, such as cellulose and lignin as well as amorphous, humified-condensation products."

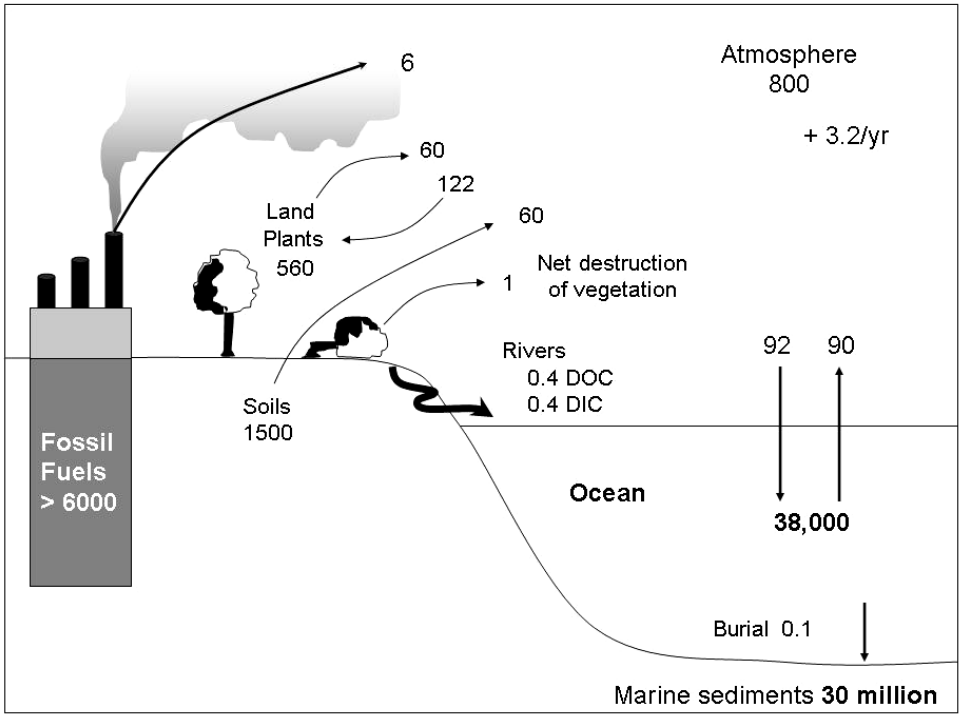


Figure 1. Global carbon cycle. All pools are expressed in units of 10^{15} g C and all annual fluxes are in units 10^{15} g C yr^{-1}, averaged from the 1980's. Slightly modified from Schlesinger, 1997.

Several pathways (Fig. 2) have been proposed for the transformation of plant biomass to humus (Stevenson, 1994): Pathway 1 is the conversion of sugars into humus, pathway 2 is the conversion of polyphenols into quinones and then to humic substances, pathway 3 is the conversion of decomposed lignin products into quinones

and then into humic substances, pathway 4 is the conversion of lignins modified by physical processes into humic substances. Note that pathways 1-3 are mediated by microorganisms, whereas pathway 4 is not. It appears that molecular bonding of secondary products with amino acids is universal to humus formation in all of the pathways outlined (Stevenson, 1994). This is most likely due to chelation, molecular bonding of secondary products with the carboxylic groups of the amino acids. The pathways that involve lignin represent the traditional view of humus formation. Stevenson (1994) postulated that not all pathways function in all ecosystems, but that one pathway may dominate in a specific ecosystem. He further suggested that a lignin pathway is the preferred pathway in poorly drained soils and wet sediments. Oxygen is required for the depolymerization of lignin, and the fungi that degrade lignin are not particularly active in excessively wet soils (Stevenson, 1994). It is thus hypothesized that wetland species that produce lignin rich biomass will lead to a greater quantity of stabilized soil organic carbon.

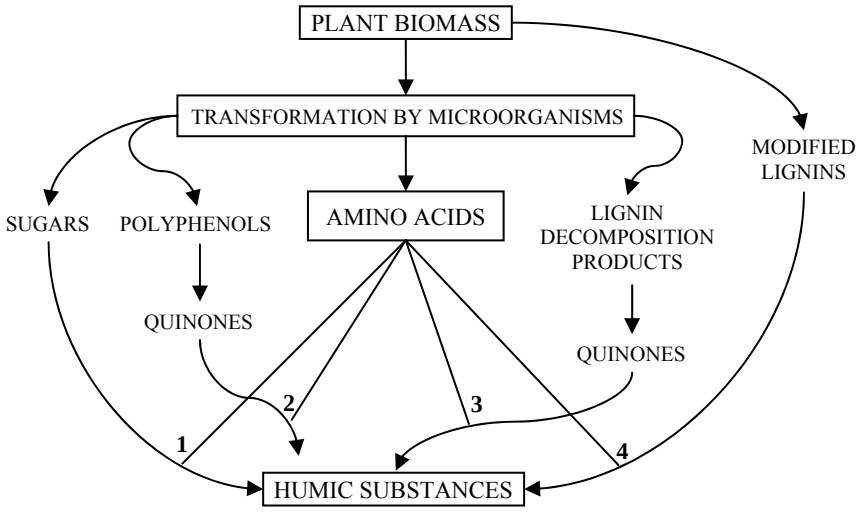


Figure 2. Pathways of humus formation. Plant constituents take these pathways en route to becoming humus. Numbers indicate pathways discussed in text. Note the importance of amino acids in all pathways. The figure was modified from Stevenson, 1994.

Wetland Invasion by Reed Canary Grass

Reed canary grass (*Phalaris arundinacea*) is an herbaceous species that has invaded riparian fringes and wetlands throughout the United States and Canada (Lavergne and Molofsky, 2004). Although *P. arundinacea* usually has a high alkaloid content, genotypes low in alkaloids have been developed for use in grazing land (Lavergne and Molofsky, 2004). In low nutrient environments, the plant tends to have a higher root/rhizome to shoot ratio compared to native species (Lavergne and Molofsky, 2004). These authors also noted that, during the months of dormancy, *P. arundinacea* stores nonstructural carbohydrates in its rhizomes. This allows the plant to tiller more prolifically the following spring. Tillers are branching shoots that germinating plants create in the sprouting stage. These extra shoots increase the shading effects experienced by other germinating competitors. Nonstructural carbohydrates consist primarily of easily degradable biochemical molecules (e.g. fructose, glucose, sucrose, and starch) that experience fast turnover times (Stevenson, 1994; Starr and Taggart, 1998). Thus, decomposition of *P. arundinacea* rhizomes containing nonstructural carbohydrates could decrease recalcitrant carbon input to soils under *P. arundinacea*, and ultimately reduce the rate of soil carbon sequestration (i.e. humus formation). However, this factor could be counter-balanced by the prolific growth and large volume of biomass produced by *P. arundinacea*. Kercher and Zedler (2004) found that noninvasive species generally produce less biomass or have shorter vegetation growth periods than *P. arundinacea* in environments experiencing deep ponding.

Species Effect on Carbon Dynamics

Because of the Kyoto protocol several countries are looking for ways to reduce net CO_2 emissions by implementing practices that lead to carbon sequestration (Gurney and Neff, 2000). The practices proposed include cropland management, rangeland management, nitrogen fertilization, and forest management. Less selective cutting of invasive species is among the proposed practices under forestry management (Gurney and Neff, 2000). If this study finds that *P. arundinacea* is significantly more apt to sequester soil carbon than native species, the negative view of *P. arundinacea* as an invasive plant may be at least partially mollified.

Jandl et al. (2007) noted that tree species occupying different ecological niches can compliment each other and, compared to monotypic stands, lead to greater organic matter formation in the long term. In particular, deep rooted species tend to deposit carbon at greater depths and, due to a lack of oxygen, deeply deposited organic matter is less susceptible to mineralization. Jandl et al. (2007) found that shallow-rooted coniferous trees sequester greater quantities of organic matter in the forest floor whereas deciduous species tend to sequester more soil organic carbon in the mineral soil. Although herbaceous stand dynamics can be different than forest stand dynamics, it is not unlikely that effects similar to those described above can be observed in wetland ecosystems.

Plant Invasion

Vitousek et al. (1996) argued that the introduction of exotic species throughout the world has resulted in widespread invasion and ecological degradation. There are at least 1,500 invasive plant species in the United States (Vitousek et al., 1996). Studies comparing the effects of invasive species on carbon and nutrient stocks are inconclusive (Hook et al., 2004; Litton et al., 2006; Kao et al., 2003; Turoff and Zedler, 2005). It appears that specific species type, regardless of its invasive or noninvasive status, and the physical environment inhabited by the species are key determinants of soil organic carbon stocks. In some cases, plant invasion increases soil carbon stocks whereas the reverse is reported in other cases. Evans et al. (2001) studied the effects of *Bromus tectorum* (cheat grass) on nitrogen dynamics in an arid grassland. They reported that cheat grass supported greater nitrogen immobilization resulting in a smaller pool of available nitrogen. Their data also showed that cheat grass biomass contained less nitrogen, yielding higher C:N and lignin:nitrogen ratios compared to native species. Evans et al. (2001) proposed that invasion of *Bromus tectorum* is self supporting. By decreasing soil available nitrogen via increased immobilization, and an increase in the frequency of wild fires by further disruption of the biological soil crust, the plant creates an environment of decreased soil fertility in which only it can persist (Evans et al., 2001). Hook et al. (2004) investigated the effects of an invasive forb on carbon and nitrogen pools at nine locations in grasslands of Montana. They found no consistent effects of the invasion on soil C and N stocks, but at locations where differences did occur, SOC stocks were depleted under the invasive forb compared to soils under the native grasses. Liao et al. (2007)

assessed the effects of invasion by *Spartina alterniflora* in the Yangtze Estuary, China. They concluded that *S. alterniflora* invasion enhanced carbon stocks in the wetland by out competing *Phragmites australis* and *Scirpus mariqueter* due to a longer growing season, higher leaf area index (LAI), and an increased photosynthetic rate. *S. alterniflora* also had higher root biomass and slower decomposition rates compared to *P. australis* and *S. mariqueter*, all these factors led to increased SOC stocks under *S. alterniflora* (Liao et al., 2007).

Objectives and Hypotheses

This review of the literature shows that several studies were conducted to assess changes in soil carbon cycling in response to invasion by exotic plant species. However, the effects vary greatly depending on the specific invasive species and the communities they invade. This study was designed to test whether invasion by *P. arundinacea* increases or decreases soil carbon stocks relative to non-invaded areas within a freshwater wetland. Ehrenfeld (2003) reported that most studies investigating the effects of exotic invasion on carbon cycling fail to compare species effects on soils inhabited by both invasive and native plant communities. To avoid this shortcoming, in the present study sampling plots were established in areas inhabited by *P. arundinacea* and native species. The specific objectives of the study are as follows:

1. Evaluate the impact of *P. arundinacea* invasion on total soil organic carbon (SOC) pools and mineralizable C in a temperate wetland complex;

2. Relate differences in SOC pools to biomass quality and wetland hydroperiod and determine which factors are dominant controls on biomass decomposition.

Consistent with these stated objectives, the following hypotheses were formulated and tested:

- Soil organic carbon stocks will be greater in areas inhabited by a mix of wetland species compared to areas supporting invasive monotypic stands of *P. arundinacea*.

- Plant communities producing the greatest amount of biomass, having the lowest residue quality, or a combination of these two factors will result in greater SOC carbon stocks. (Fig. 3)

- Areas experiencing ponding most frequently will sequester more SOC as a result of O_2 depletion.

The following tasks were completed to test these hypotheses: monitor wetland hydroperiods during the entire study; survey selected plant communities to determine species distribution and diversity; collect above and below-ground biomass to determine biomass input; analyze above and below-ground plant tissues to determine their biochemical composition (i.e. proximate cellulose, lignin, and total phenolics); conduct laboratory incubations using plant matter collected in the field as a model of in situ decomposition.

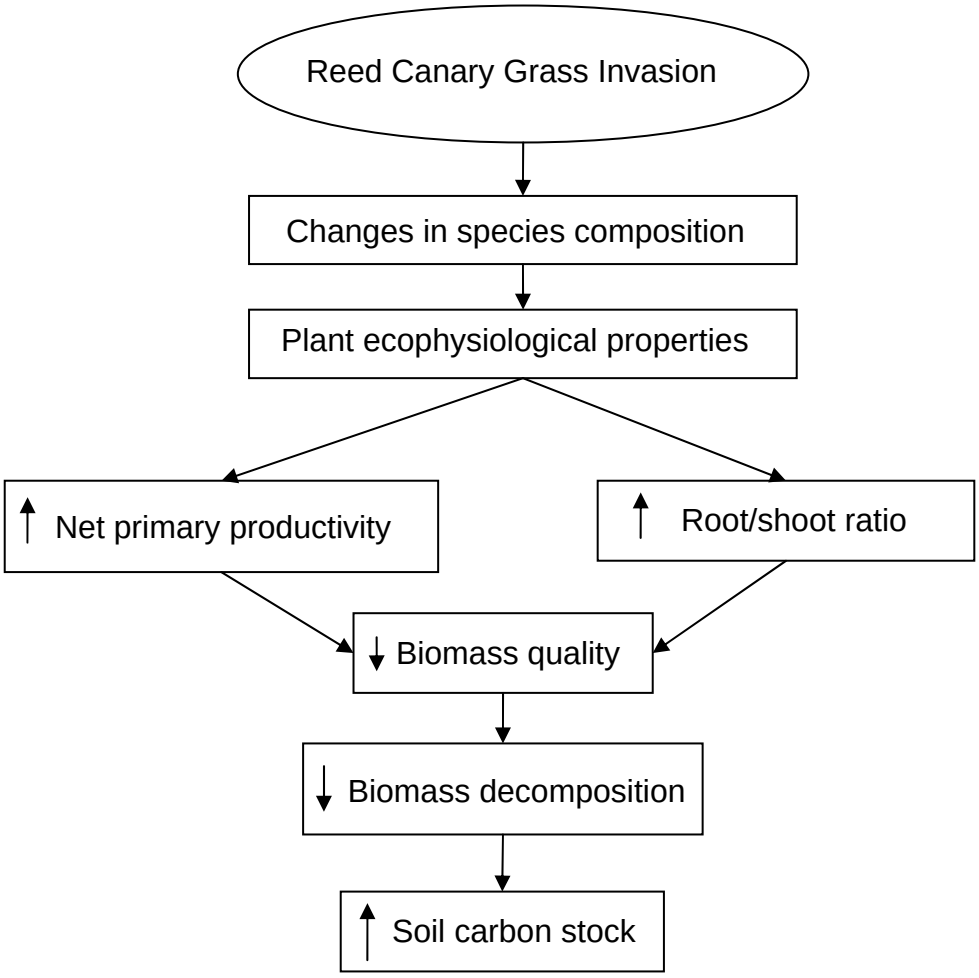


Figure 3. Carbon sequestration by *P. arundinacea* – A conceptual model. It was expected that if *P. arundinacea* exhibited growth patterns like those outlined above, an increase in SOC pools would result under the invasive grass. It is generally accepted that lower biomass quality (i.e. high lignin and phenol concentrations in plant biomass) reduces decomposition rates leading to increased deposition of condensation products in the soil profile.

STUDY SITE

Geologic Setting

"Beanblossom Bottoms" is a wetland complex in south-central Indiana, located 45 miles southwest of Indianapolis (Lat: 39.280342, Long: -86.574905) and bordered at its southern edge by Beanblossom Creek which runs in a westerly direction across northern Monroe County, Indiana. Beanblossom Bottoms is shaped as a bowl (mean elevation 173 m asl) surrounded by hilly terrain (elevation: 215-245 m) on almost all sides. Beanblossom Creek acted as a sluiceway for outwash material during the retreat of the Illinoian ice (Thornbury, 1950). During the Illinoian glaciation, the creek's western drainage was blocked by a lobe of ice; forming a periglacial lake (Thornbury, 1950). Outwash from the later Wisconsinan glaciation did not intercept Beanblossom Creek's drainage; the presence of glacially derived sediments at Beanblossom Bottoms is strictly due to the Illinoian glaciation. Therefore, soils (Fig. 4) at Beanblossom Bottoms are formed in Illinoian age glacial till; consisting predominantly of silt and clay.

The three dominant soil series at Beanblossom Bottoms include Bonnie (fine-silty, mixed, active, acid mesic Typic Fluvaquent), Stendal (fine-silty, mixed, active, acid, mesic Fluventic Endoaqept), and Zipp (fine mesic Endoaquepts) (NRCS, 2007). It is noted that the slightly coarse-textured Bonnie and Stendal series are mapped closer to Beanblossom Creek. This probably reflects the influence of over bank deposits on the development of the Bonnie and Stendal soils, whereas the fine-textured Zipp soils seem influenced by slack water deposits. Water table information from the NRCS soil survey (NRCS, 2007) indicated that ponding occurs frequently

between December and May in the Zipp (up to 30 cm depth) and Bonnie (up to 15 cm depth) soil series. Although frequently flooded, according to the soil survey, ponding does not occur in areas occupied by the Stendal soil series.

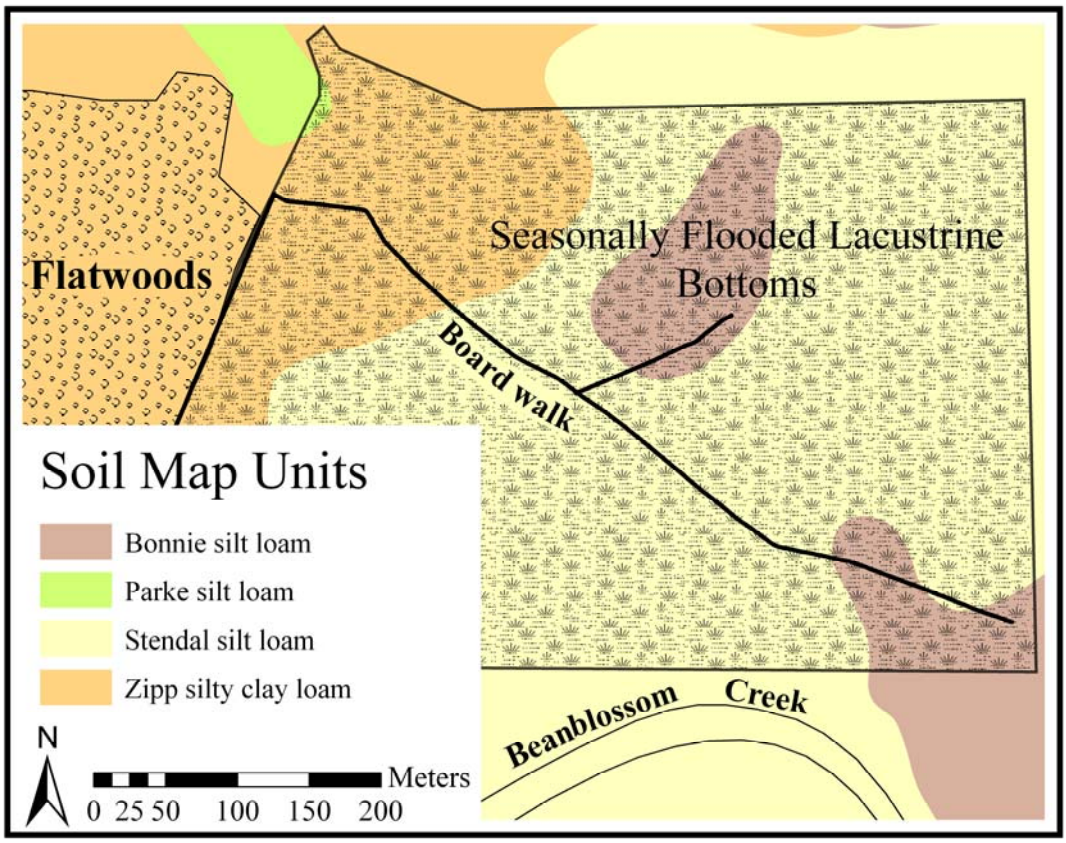


Figure 4. Soil map of study site. Mapped by the Natural Resources Conservation Service.

Climate

Central Indiana receives an average of 114 cm (45 inches) precipitation annually (NASA, 2007). Average monthly precipitation ranges from 7 cm (2.7 inches) to 12 cm (4.6 inches) with the highest average monthly precipitation in May and the lowest in February (NASA, 2007). Average annual temperature in central Indiana is 11.65 °C (53 °F) (Indiana State Climate Office, 2008). The hottest month is July with an average temperature of 24.3 °C (75.7 °F) and the coldest month is

January with an average temperature of -1.8 °C (28.8 °F). The average temperature during the growing season is 18.7 °C (65.7 °Fahrenheit) (Indiana State Climate Office 2008).

Land-use History

The study site within Beanblossom bottoms was cropland prior to its acquisition by Sycamore Land Trust in 1997. An internal memo received at the time of acquisition in 1997 indicated that the 24 hectares (60 acres) constituting the current study site were abandoned in 1992 (personal communication, John Lawrence, Assistant Director, Sycamore Land Trust, May 21, 2008). Therefore, the plant communities present at Beanblossom Bottoms had 10 to 15 years to become established prior to sampling.

Hydroperiods at Beanblossom Bottoms

Preliminary field reconnaissance at Beanblossom Bottoms indicated the occurrence of *P. arundinacea* in areas of different hydrologic regimes; some areas pond more frequently and flood to deeper depths than other areas. Several authors have reported that vegetation communities are affected by depth, duration, and periodicity of ponding (Mitsch and Gosselink, 2000; Kercher and Zedler, 2004); therefore the study was designed to incorporate hydrology as a factor regulating plant physiology and in turn soil carbon stocks in the wetland. As noted, excessively wet areas also inhibit the growth of fungi and bacteria responsible for degrading lignin. To account quantitatively for apparent differences in wetland hydroperiod, monitoring wells were established to characterize site hydroperiod, defined as the seasonal variation of the water table of a wetland (Mitsch and Gosselink, 2000).

MATERIALS AND METHODS

Sampling Design and Plot Installation

In accord with the study objectives, four study areas were established at the wetland complex where extensive soil and vegetation sampling was conducted (Fig. 5). Each study area consisted of a 10 m diameter plot, and within each plot three (3) quadrats (1 m x 1 m) were defined. Study plot selection was primarily guided by vegetation types (*P. arundinacea vs. native species*) within broad areas expected to experience either frequent or infrequent ponding. These sampling plots, as outlined below, were established within the study site on April 25, 2007 (Fig. 5).

- Plot 1: Species: *P. arundinacea*. Expected hydrology: infrequent ponding.
- Plot 2: Species: Mixed Natives. Expected hydrology: infrequent ponding.
- Plot 3: Species: *P. arundinacea*. Expected hydrology: frequent ponding.
- Plot 4: Species: Mixed Natives. Expected hydrology: frequent ponding.

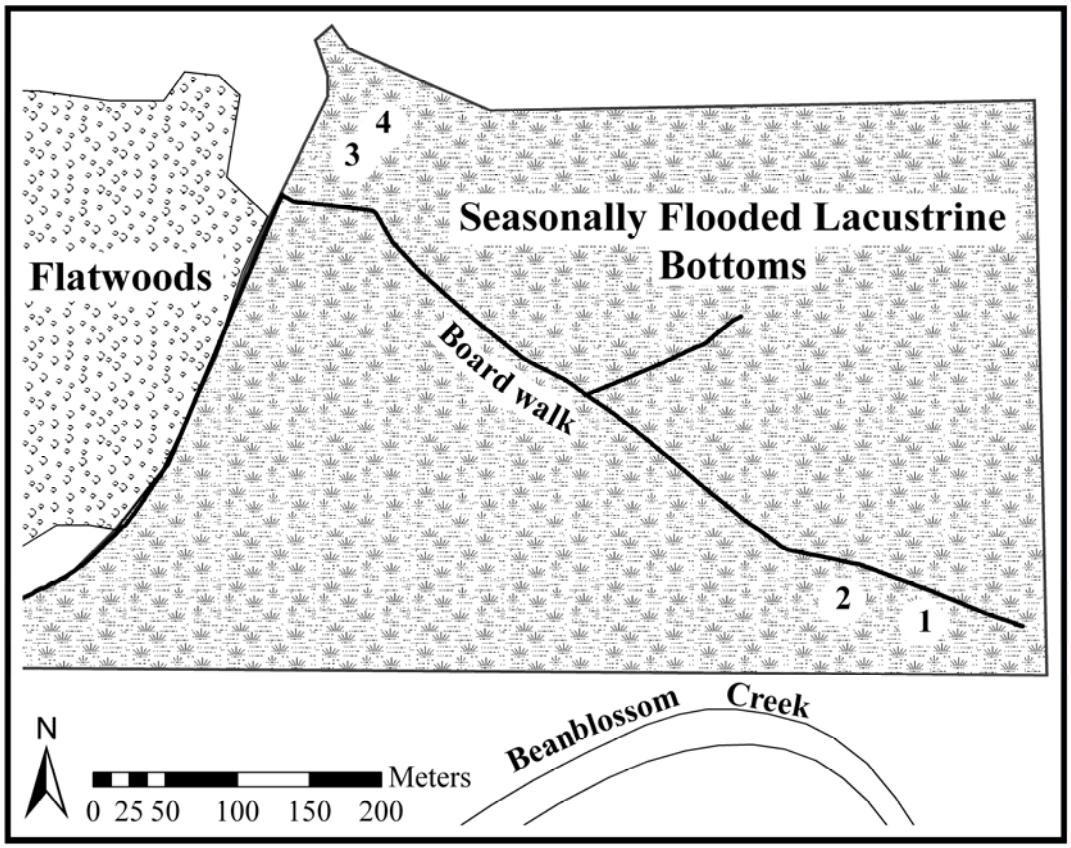


Figure 5. Map of study site. The study site is located within Beanblossom Bottoms Nature Preserve. Numbers indicate the location of study plots. Initial field reconnaissance suggested that plots 1 and 2 experienced infrequent ponding, and plots 3 and 4 experienced frequent ponding. At the time of establishment, plant communities were recorded as follows: Plot 1, invaded by *P. arundinacea*; Plot 2, inhabited by a mix of native species; Plot 3, invaded by *P. arundinacea*; Plot 4, inhabited by a mix of native species.

Plant Survey

A vegetation survey was conducted at each of the study plots to assess percent relative cover and species composition. Additional quadrats were surveyed in each plot until the minimum area of cover needed to quantify species distribution and dominance was determined (Tiner, 1999). Three (1 m x 1 m) quadrats were designated within the study plots for plant and soil sampling. These quadrats were located so that they are representative of species composition in each plot. Relative

species cover was determined for each of the sampling quadrats. All plant survey activities were completed before plant and soil sampling was begun.

Prevalence Index for Distinguishing Wetland Hydrology

The United States Department of Agriculture classifies plant species based on their frequency of occurrence in wet versus dry environments. This classification is referred to as a species wetland indicator status. Wetland plants are categorized as obligate wetland (OBL), facultative wetland (FACW), facultative (FAC), facultative upland (FACU), and obligate upland species (UPL), where: OBL, occur in wetlands 99% of the time; FACW, occur in wetlands 67% of the time; FAC, are equally likely to occur in wetlands or non wetlands; FACU, occur in wetlands 33% of the time; and UPL, occur in wetlands 1% of the time (USDA, 2008).

Tiner (1999) described a method whereby the wetland indicator status of each plant in a community is used to develop an index of wetness for the soils that the plant community inhabits. The wetland indicator status of each plant is given a specific rating (OBL = 1; FACW = 2; FAC = 3; FACU = 4; UPL = 5). This rating is multiplied by the percent cover of a specific species and all values are summed. This sum is divided by the sum of covers (i.e. 100% in our case). Values obtained for this index range from 1 to 5 with 1 representing wetlands and 5 representing well drained upland ecosystems. Each plot was assigned a prevalence index to further define wetland hydrology at the site.

Well Installation

Shallow wells were installed (Appendix A) in plots 1, 2, and 3 to characterize wetland hydroperiods. There was no well installed in plot 4 because on the day of

installation, April 25th 2007, the water level above the ground surface in plots 3 and 4 differed by only 5 cm. Also, the distance between well 3 and the center of plot 4 is only 21 meters. It was concluded, based on these observations, that plots 3 and 4 have similar hydroperiods. Methods of installation were slightly modified from those outlined by the Wetlands Regulatory Assistance Program (ERDC TN-WRAP-00-02). Wells were installed to a depth of 1 meter with stickups of 65 cm. The wells are slotted their whole length from the terminus to the top of the riser; this allowed the *Solinst* level loggers, which operate by sensing increases in hydrostatic pressure with depth, to record water depths that overtopped the risers of each well. Filter sock made of geotextile fabric was used to prevent clogging of the wells by silt and clay. On June 16, 2007 Solinst level loggers were installed in each well and set to take measurements continuously on a 15 minute interval for the duration of the study. Each level logger was positioned 143 cm below the top of each well with a wire string (Appendix A).

Field Sampling

Above-ground Biomass Sampling

Above-ground biomass was sampled from each of the three quadrats in each plot twice during the growing season. The first sampling occurred in the middle of the growing season (July 11-18, 2007) and the second sampling occurred at the end of the growing season (October 29 and November 1, 2007). This sampling scheme was designed to test the effect of growth phase on biochemical composition and the quantity of biomass produced. Each quadrat was separated into two equal rectangles; biomass was retrieved from one half of each quadrat in the middle of the growing

season and the other half at the end of the growing season. Vegetation was retrieved by cutting stems and leaves off at the ground surface and storing them in 30 gallon paper bags for transport back to the laboratory. Upon arrival at the laboratory vegetation samples were transferred into wire mesh bags and oven dried (60 - 70 °C, 48 h). Dried vegetation biomass was then ground using a blender and the pulverized material was passed consecutively through a 212 and a 150 µm sieve. The < 150 µm fraction was used for C/N analysis whereas the (150-212) µm fraction was used for biochemical tests including assays for lignin, cellulose, and total phenolic content. These analyses were conducted on biomass obtained at the middle and end of the growing season.

Below-ground Biomass Sampling

Root biomass was retrieved from each quadrat using a 9 cm diameter soil coring device (Giddings Machine Company, Windsor, Colorado). The device was driven into the soil profile using a sledge hammer. Soil cores were divided into three 5-cm intervals (0-5 cm, 5-10 cm, 10-15 cm) and one 15-cm interval (15-30 cm). The root cores were divided into these four intervals to determine if differences exist between the root distributions of *Phalaris arundinacea* and native species.

Root biomass was separated from the soil by wet sieving, air dried for at least 48 hours and then placed in a 60-70 °C oven for 48 hours until dry. Root density (g root cm^{-3}) was computed for each soil depth interval as the dry weight of root material divided by the core volume over that specific interval. After roots from each interval were weighed individually, the roots from all 30 cm were combined and ground using a blender to pass through 212 and 150 µm sieves consecutively. The

< 150 μm fraction was used for C and N analysis and the (150-212) μm fraction was used for biochemical tests.

Soil sampling

Soil samples were collected in the middle of the growing season concurrently with the first biomass sampling. Soil samples were obtained with a 2 cm diameter soil probe. Two soil cores were sampled from each quadrat as replicates to increase the accuracy of soil carbon data. Soil sub samples of 5 cm increments were placed in individually labeled zip seal bags and kept on ice for transport back to the laboratory. The upper 15 cm was sampled in 5 cm intervals (0-5, 5-10, and 10-15 cm) while the lower 15 cm (15-30 cm) was combined in one sample. Soil samples were air dried for one week before being crushed with mortar and pestle to pass a 150 μm sieve. These soil samples were then analyzed for total C and N by dry combustion (960 °C) using a flash EA 1112 series CHNS-O analyzer (Thermo Scientific, Waltham, Massachusetts).

Soil Physiochemical Properties

To determine the bulk density of soil within each quadrat, one soil core (5 cm diam, 30 cm long) was taken and divided into 5 cm intervals to a depth of 15 cm and then divided into two 7.5 cm intervals below that depth. Cores were oven dried for 72 hours at 65 °C or until a constant dry weight was obtained. Bulk density (g cm^{-3}) was then calculated for each soil depth interval as soil dry mass divided by sample volume. Soil material from each core was extruded by hand and used for soil texture and pH analysis.

The texture of soils at Beanblossom Bottoms was assayed using the hydrometer method (Gee and Bauder, 1986). Oven dry soil samples from each quadrat were crushed and passed through a 2 mm sieve to remove the gravel-size fraction. After crushing 50 gram portions of each soil was placed in a 250 mL beaker and treated with 30 mL of 30% H_2O_2 to oxidize organic matter. The 30 mL of H_2O_2 were added in three doses of 10 mL each after the previous dose had boiled away. After all the H_2O_2 was boiled off, the soil was transferred quantitatively to 250 mL nalgene bottles and treated with 50 mL of (5%) sodium metaphosphate. Samples were shaken overnight on a Barnstead Lab-Line Max-Q 2508 orbital shaker at a moderate speed. After shaking, the samples were transferred quantitatively to 1000 mL plastic graduated cylinders and brought up to 1000 mL with de-ionized water. Cylinders were covered with parafilm and inverted and shaken vigorously to suspend all sediments. A Barnstead ERTCO #2153A-BF hydrometer calibrated at 20 °C was inserted in the suspension immediately after inversion. After 40 seconds, a reading was recorded as a measure of silt and clay content suspended in solution. After 3 hours the hydrometer was reinserted and its reading was recorded to determine clay content. Temperature was recorded at both the 40 second and three hour measures to correct for viscosity effects. Sand, clay and silt were calculated as follows:

$\text{Sand} = 100.0 - [H_1 + 0.2\,(T_1 - 68) - 2.0] \times 2$

$\text{Clay} = [H_2 + 0.2\,(T_2 - 68) - 2.0] \times 2$

$\text{Silt} = 100.0 - (\%\ \text{sand} + \%\ \text{clay})$

Where: H1 = hydrometer reading at 40 seconds

T1 = temperature reading at 40 seconds

H2 = hydrometer reading at 3 hours

T2 = temperature reading at 3 hours

0.2 = temperature correction based on number of degrees away from 20 °C

-2.0 = Salt correction to be added to hydrometer reading

The calculations for sand and clay are multiplied by 2 because only 50 grams soil was used in the analyses and this doubles those values to obtain a proportion of 100%.

Moisture retention (Klute, 1986) of soils from study plots A and B were also evaluated. Small 5 cm x 5 cm x 5 cm soil cores were sent to the University of New Mexico for analysis of soil water release characteristics (Klute, 1986). The soil cores were analyzed for moisture content at saturation and field capacity. These measurements were used to model moisture regimes of the two soils used in the decomposition experiment.

Biochemical Properties of Plant Biomass

Plant biomass (sampled at the middle and end of the growing season), including above and below-ground biomass, was analyzed for total C and N, proximate cellulose, proximate lignin, and total phenolics.

Cellulose and Lignin Assays

Above and below-ground biomass from each quadrat was analyzed for acid detergent fiber, proximate cellulose, and proximate lignin using gravimetric methods outlined by Graca et al. (2005). An acid detergent extracting solution was prepared by dissolving 20 grams cetyl trimethyl ammonium bromide (CTAB) in 1000 ml of 0.5 M H_2SO_4. Approximately 245 to 265 mg of plant biomass were weighed into 30 ml screw-top glass test tubes for extraction. Each sample was treated with 20 ml acid

detergent and 0.4 ml reagent grade decahydronapthalene. Extraction tubes were then placed in a hot (~100 °C) water bath for 3 hours to extract acid detergent fiber. Each sample was then filtered quantitatively using a Gooch crucible that was pre-combusted (550 °C) and weighed to the nearest 0.1 mg. The nominal pore size of the Gooch crucibles (Pyrex, 50 ml high form) used in these analyses was between 4 and 5.5 µm. Each crucible was firmly set on a 1000 ml Erlenmeyer flask and taped in place (electrical tape) to create a seal between the flask and the crucible. Crucibles were filtered in sets of six. Acid resistant plastic tubing and connectors were used to connect all six flasks to a moisture trapping flask that than led to a Varian SD90 rotary vacuum pump. Samples were pumped until all acid detergent was drawn away and rinsed generously with hot (90-100 °C) deionized water. Each sample was then rinsed with acetone until no color was observed in the leachate. Crucibles were then removed from the filtering apparatus and dried overnight at 105 °C. After cooling for one hour in a desiccator, samples were weighed to the nearest 0.1 mg. Each crucible containing dry sample material was then placed in an acid-resistant dish and treated with 72% H_2SO_4 for 3 h. The level of acid in each crucible was maintained so that the sample was covered constantly during the 3 h treatment. Crucibles containing acid treated samples were then placed on the filtering apparatus as before and pumped until all H_2SO_4 was drawn away. Two generous doses of hot (90-100 °C) deionized water were then administered; washing the sample free of acid. Crucibles were then removed and dried overnight in a 105 °C oven as before. After cooling for 1 hour in a desiccator, each crucible containing oven dried H_2SO_4 treated sample was weighed to the nearest 0.1 mg. After weighing, the crucibles were ignited in a muffle furnace at

550 °C for 3 h to remove the proximate lignin fraction. Crucibles were then allowed to cool overnight in a desiccator before weighing to the nearest 0.1 mg. Each biomass sample was processed in duplicate. Replicates displaying a coefficient of variation greater than 2 were reprocessed. Acid detergent fiber, proximate cellulose, and proximate lignin were calculated following Graca et al., 2005:

$$\frac{W_0 - W_t}{W_s} \cdot 100 = ADF$$

where: W_0 = weight of the oven-dry crucible including fibre
W_t = tared weight of the oven-dry crucible
W_s = oven-dry sample weight.

$$\frac{L_a}{W_s} \cdot 100 = ADC$$

where: L_a = loss due to 72% H_2SO_4 treatment
W_s = oven dry sample weight.

$$\frac{L_i}{W_s} \cdot 100 = ADL$$

where: L_i = loss upon ignition after 72% H_2SO_4 treatment
W_s = oven-dry sample weight

Total Phenolics Assay

Above and below-ground biomass collected from each quadrat at the middle and end of the growing season was analyzed for total phenolics using the Folin-Ciocalteu method as outlined in Graca et al. (2005). A standard curve was created as follows. A stock solution (600 µg tannic acid ml^{-1}) was prepared by dissolving 60 mg

reagent grade tannic acid powder in 100 ml acetone (30% water, 70% acetone). The following fractions of the stock solution were placed in glass test tubes: 0.00, 0.01, 0.02, 0.05, 0.1, 0.2, 0.4, 0.6, 0.8, and 1 ml. Each of these tubes was amended with de-ionized water to bring them to a volume of 1 ml. Therefore, the amount of tannic acid in each of these tubes was 0, 6, 12, 30, 60, 120, 240, 360, 480, and 600 µg, respectively. A solution of 2% Na_2CO_3 dissolved in 0.1 N NaOH was prepared to be used as a reactant. Five ml of this solution was added to each test tube. After 5 minutes, 0.25 ml Folin-Ciocalteu reagent was added to each tube. After the addition of Folin-Ciocalteu reagent, 120 minutes were allowed for color development. Triplicate 200 µl aliquots from each test tube were transferred into microplate wells. Their absorbance (λ=760 nm) was read on a VERSAmax tunable micro plate reader (Molecular Devices Sunnyvale, California, 94089). Average absorbance was plotted against µg tannic acid in each test tube. A straight line ($y = 348.76x – 29.376$) was obtained (r^2: 0.99). Y is equal to µg tannic acid and x is equal to absorbance at 760 nm.

One hundred mg samples of oven dry biomass were extracted with 5 ml acetone (30% water, 70% acetone) in 10 ml Teflon centrifuge tubes for one hour at 4 °C. This was followed by centrifugation at 16,000 rpm and 4 °C for 20 minutes on a Beckman Coulter XL-90 centrifuge with type 90Ti rotor rated for 90,000 rpm. After centrifugation, 0.5 ml of each solution was removed and amended with 0.5 ml of de-ionized water in glass test tubes. Each solution was then treated with Na_2CO_3 and Folin-Ciocalteu reagent just as in the calibration above, and read on the plate reader after 120 minutes. Stock solutions containing 60 and 360 µg tannic acid were

analyzed with each phenolics assay. The average concentration calculated for the 60 µg tannic acid stock solution across all phenolic assays on all days was 64.162 µg with a coefficient of variation of 10%. The average concentration calculated for the 360 µg tannic acid stock solution across all phenolic assays on all days was 394.19 µg with a coefficient of variation of 5.5%.

Decomposition Study

Incubation is a commonly used approach to study plant biomass decomposition (Fog, 1988; Janssen and Walker, 1999; Evans et al., 2001; Michel and Matzner, 2002; Johnson et al., 2007; Hagedorn and Machwitz, 2007). The incubations in this study were conducted in the laboratory and modeled after those outlined by Johnson et al. (2007). The purpose of the incubation was to assess biomass decomposition and quality.

Composite soil samples (10 cm depth) obtained from the two native species plots (2 and 4) were used in the decomposition study. Ground biomass (2-3.4 mm) from plots 1 and 2 was incubated using soil collected from plot 2 and ground biomass collected from plots 3 and 4 was incubated in soil collected from plot 4. Approximately 100 g of field moist soil was weighed in glass jars (V = 900 mL). Before transferring into the jars, soil was homogenized by mixing by hand in a 10 gallon bucket and then was passed through a 2 mm sieve to remove roots and gravel.

Biomass (above and below-ground) from the following plant species was included in the study: (i) *P. arundinacea* and mixed native species from plots 1 and 2 respectively; (ii) *P. arundinacea* and *Scirpus cyperinus* from plots 3 and 4 respectively. Thus, the incubation study included two (2) soil types, two (2) plant

organs (i.e. above and below-ground biomass), and four (4) plant types for a total of 16 treatments. Each treatment was run in triplicate. Because lesser amounts of below-ground biomass were generally available, 1 g of root biomass was added whereas 2 g of above-ground material was used. Each type of biomass was mixed with 100 g sieved soil. Three controls, containing sieved soil only from each soil type, were also included in the incubation study. Above and below-ground biomass from each species was analyzed for total C, N, cellulose, lignin, and phenolics. Using information from the water release analysis, incubation involving soils from plot 2 and plot 4 was conducted at soil moistures of 35 and 42 grams H_20 per 100 grams soil, respectively (the average of soil moisture at saturation and field capacity). Deionized water was added to each jar to obtain the desired moisture content. Throughout the incubation experiment, jars were weighed to account for moisture loss and deionized water was added as needed.

Jars were sealed with screw-top lids fitted with butyl rubber septa and incubated at 18.7 °C, the long-term (1950-2007) mean temperature during the growing season (April thru October) in south-central Indiana (courtesy of NASA, 2007). The incubation lasted for 154 days (September 18, 2007 - May 15, 2008). Analysis of jar headspace for CO_2 production occurred on days 2, 3, 4, 6, 8, 11, 14, 16, 19, 21, 23, 28, 34, 42, 47, 58, 70, 81, 92, 109, 126, and 154. The CO_2 gas produced was analyzed using a Varian CP3800 gas chromatograph equipped with a thermal conductivity detector. Preliminary tests suggested that the incubation jars could become anoxic within 3-4 days. To avoid this, each jar was opened and allowed to vent for 1 h after each sampling occasion. Sampling intervals increased later during

the experiment as microbial activity appeared to level off around 60 days after the start of the incubation. The CO_2 that was produced between each venting was added to the total CO_2 produced in each previous sampling. This resulted in a record of cumulative CO_2 production for each treatment. The following equation was used to convert ppm CO_2 to mg CO_2 – C (Jacinthe and Groffman, 2001). Note that one ppm is equivalent to one microliter L^{-1}.

$$\frac{\mu L\ CO_2}{L} \times \frac{O.84\ L}{1} \times \frac{1.97\ \mu g\ CO_2}{\mu L\ CO_2} \times \frac{1\ mg\ CO_2}{1000\ \mu g\ CO_2} \times \frac{12}{44} = mg\ CO_2 - C$$

With 0.84 liters representing the headspace of each jar, 1.97g cm^{-3} representing the density of CO_2, and the proportion 12/44 representing a conversion to remove the oxygen component of CO_2 and leave only the mass of carbon. The result is mg C evolved as CO_2. The quantity of residue carbon added was determined by multiplying the percent C obtained in plant C and N analysis by the mass of residue added; (2 grams above-ground biomass, 1 gram below-ground biomass respectively). Percent carbon loss was calculated as the mass of carbon respired divided by the mass of biomass carbon added.

Statistical Analyses

ANOVA were performed using the PROC GLM Procedure available in SAS. After each ANOVA, post hoc t-tests were performed for separation of means. Sample sets not large enough for ANOVA were compared using paired t-tests in SigmaPlot. Unless otherwise noted, statistical significance was determined at the 95% confidence level.

RESULTS

Site Hydroperiod

The three monitoring wells installed at the study site showed that plant communities at Beanblossom Bottoms experience three distinct hydroperiods (Figs. 6, 7, and 8). Water levels recorded during the 2007 growing season were much lower than levels recorded during the 2008 growing season; water tables differed marginally among plots during summer and fall 2007. However, in 2008, marked differences among the plots were observed in both growing and dormant seasons. In plot 1, the water table remained above the ground surface during all of spring 2008 (Fig. 6), and averaged 3.5 cm below the ground surface during the first half of the growing season. In plot 2, the water table resided at an average depth of 23 cm below the ground surface during the 2008 growing season, whereas in plot 3 the average water table depth was 13 cm above the ground surface during the first half of the 2008 growing season. During the 2008 dormant season, the water table in plot 1 resided at an average depth of 12 cm above the ground surface whereas in plot 2, it resided at an average depth of 7 cm below the ground surface. During that same period (dormant season 2008), plot 3 and 4 were periodically flooded (depths up to 76 cm above the ground surface) and also experienced significant water table drawdown (Fig. 8). Breaks in each hydrograph (Figs. 6-8) represent periods when the water table dropped below the base of the well, 87 cm below the ground surface. In plot 1 the water level was detectable from June 2007 to the first week of August 2007; however the water level fell below the base of the well for the rest of August through early December 2007. In plot 2 the water level resided below -87 cm from the start of monitoring in

June 2007 until mid December 2007. In Plot 3 the water level remained above -87 cm from the start of monitoring in June 2007 until August 12, 2007 when it fell below the base of the well until early December (except for a one week period in late October when the water table responded to a precipitation event). Water levels in all three plots remained above 87 cm below the ground surface from early December 2007 through August 2008.

After examination of the wetland hydrographs (Figs. 6-8), the following descriptions were arrived upon to represent the hydroperiods that plant communities experience during the growing season at Beanblossom Bottoms. Plot 1 is seasonally ponded, plot 2 is seasonally saturated and plots 3 and 4 are variably flooded with deep (> 50 cm) water (Figs. 6, 7, and 8).

Figure 6. Wetland hydrograph – Plot 1. *P. arundinacea.* Breaks in the hydrograph represent periods when the water table was below the base of the well at 87 cm below ground surface.

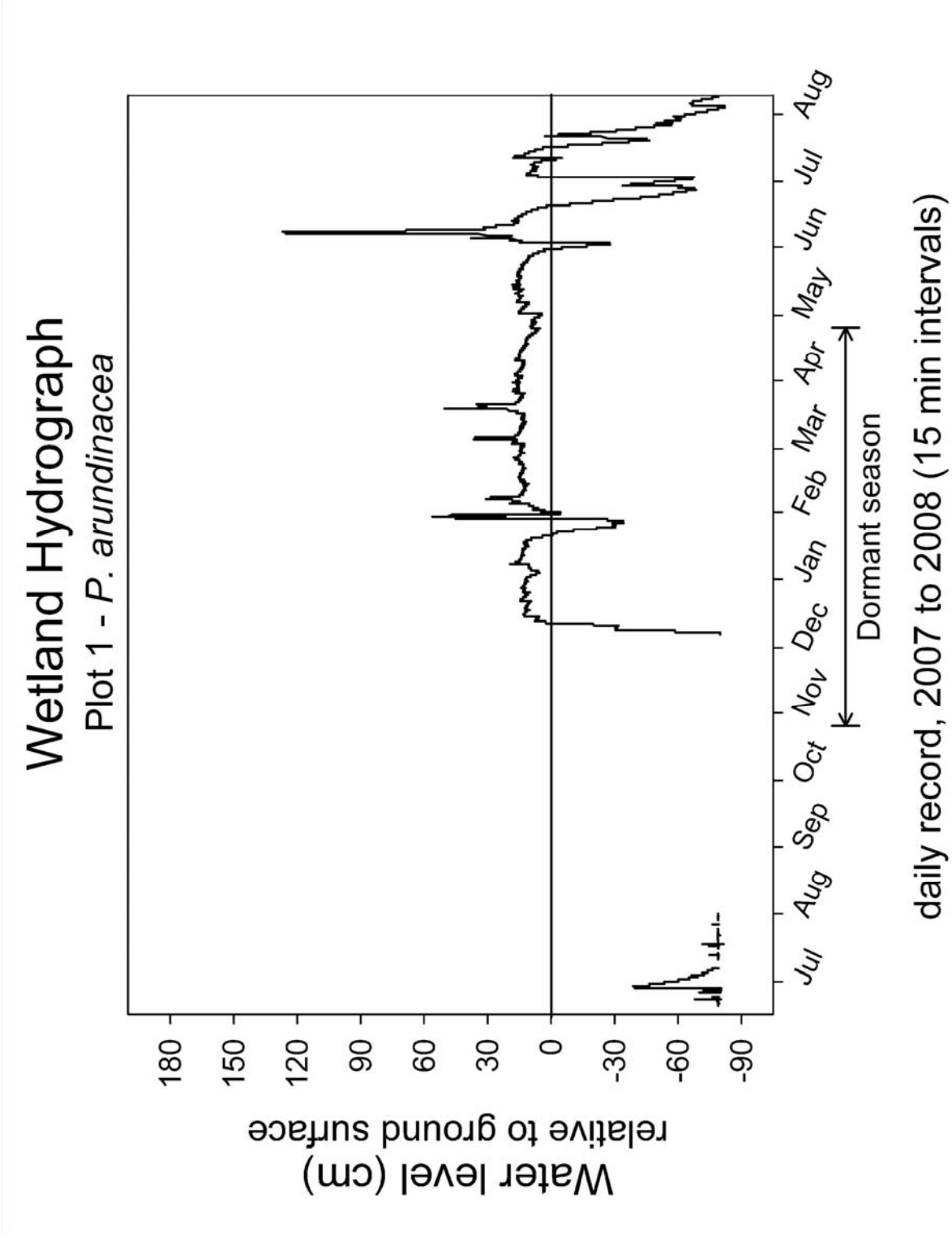


Figure 7. Wetland hydrograph – Plot 2. Mixed native plants. Breaks in the hydrograph represent periods when the water table was lower than the base of the well at 87 cm below ground surface.

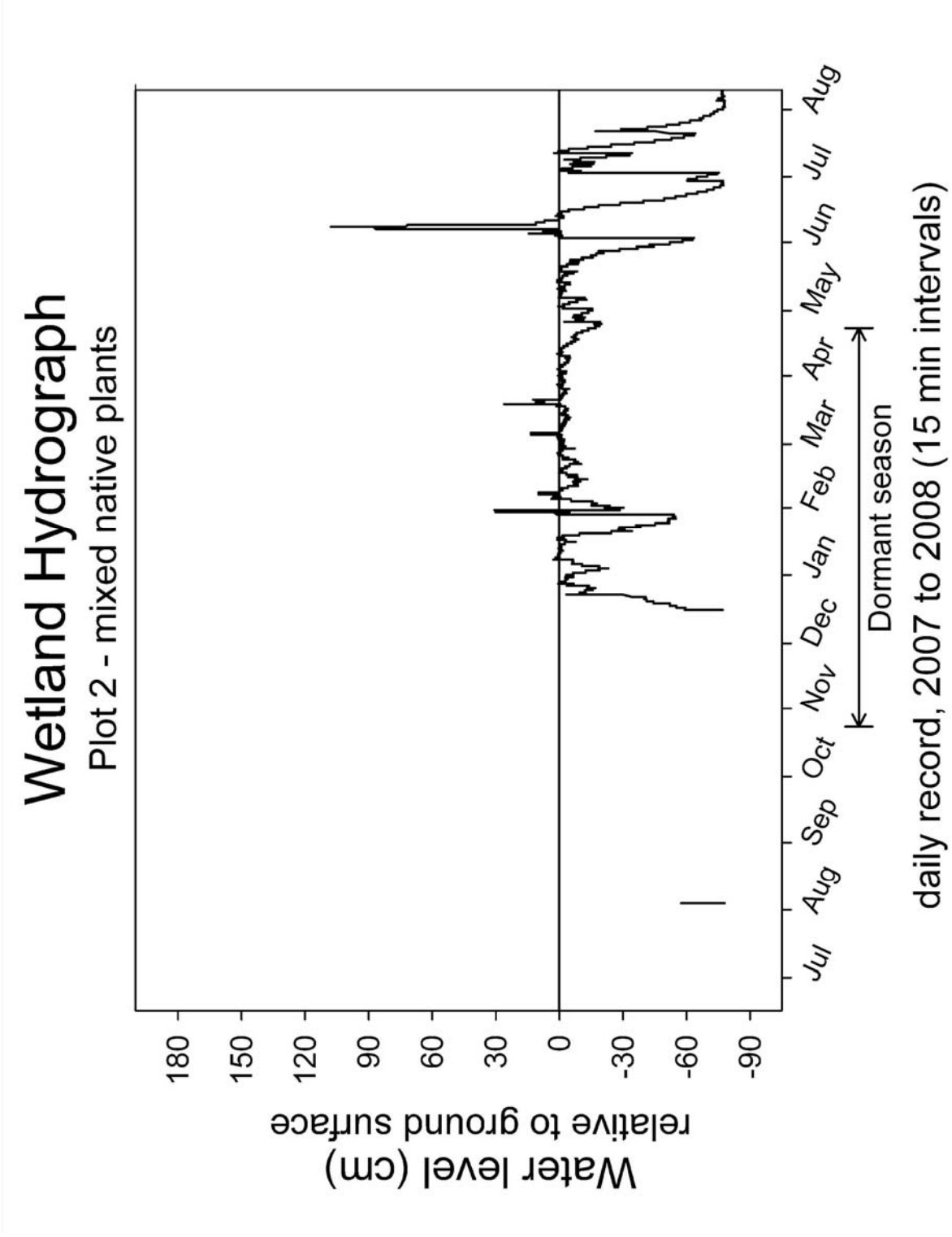
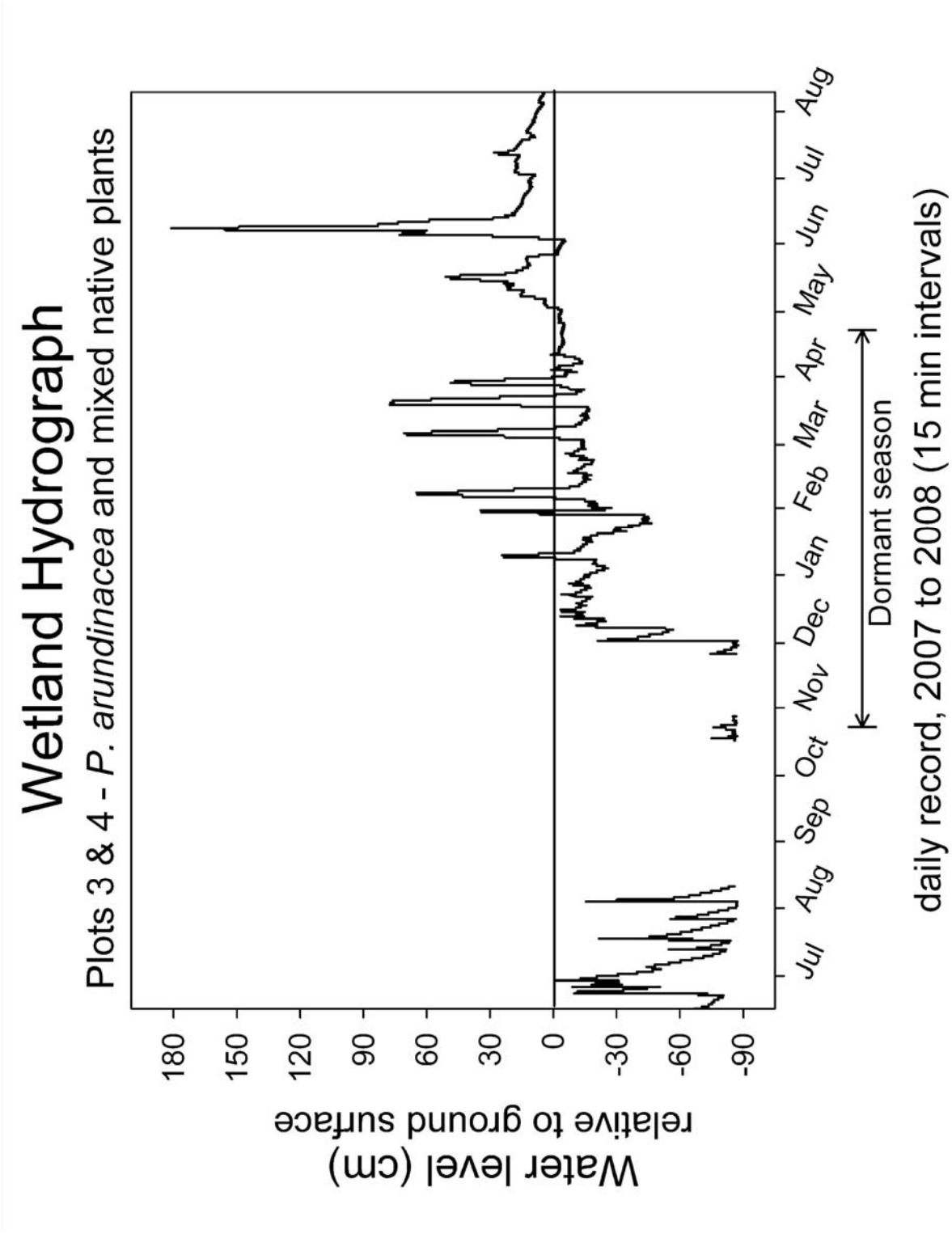


Figure 8. Wetland hydrograph – Plots 3 and 4. *P. arundinacea* and mixed native plants. Breaks in the hydrograph represent periods when the water table was deeper than the base of the well at 87 cm below ground surface.



Plant Communities and Their Nomenclature

The initial study design anticipated that plots 1 and 2 were installed in areas of infrequent ponding and plots 3 and 4 were installed in areas of frequent ponding. The original study design was straight forward with regard to plant communities as well. However, the hydrology, as described above, and the distribution of plant communities at the site proved to be much more complex than the original design (see description, p. 15).

While plant communities surveyed met the demands of the original study design, comparing *P. arundinacea* invaded and mixed native plant communities, the composition of native plant communities was considerably more complex than anticipated. Plots (1, 3) invaded by *P. arundinacea* were both characterized as monocultures during the plant survey as expected; however, native stands were more complex. Plot 2 contained 24 different native plants with four species dominating (50% relative cover) the plot; Plot 4 consisted of only two obligate wetland plant species with one dominating (74% relative cover) the plot. Analysis of the hydrology of each of these plots resulted in three hydrologic regimes. Therefore, the original data analysis approach was modified and replaced with a new plan that still accounted for hydrology and plant community structure within the study plots. In accordance with this new plan, plot numbers were replaced with letters, and comparison of soil properties and C stocks among various sections of the wetland were made according to the statistical scheme outlined in Table 1.

On the basis of the plant survey and site hydrology, the following four vegetation communities were considered in the study (Table 1). Community A

consisted of a mixed native assemblage inhabiting seasonally saturated soils with *Carex lurida*, *Juncus effusus*, *Solidago canadensis*, and *Juncus interior* having co-dominance (Table 2). Community B was a low diversity native plant community inhabiting variably flooded soils, *Scirpus cyperinus* and *Juncus effusus* had co-dominance in this plot (Table 3). Community C was a variably flooded area of the wetland dominated by *P. arundinacea* (Fig. 9). Plant community D, consisted of a nearly monotypic stand of *P. arundinacea* (92%) (Table 4) located in a seasonally ponded section of the wetland.

Because plant community A does not inhabit the same soil type, or have the same hydrology or assemblage of plants as any other study plot it was used as a native species reference plot to make general comparisons with the other three plots. Native plant community B and invasive plant community C occur on the same soil series (Zipp) and experience the same wetland hydroperiod, therefore, they were used to assess the effect of plant species on carbon storage. Plant community C and plant community D are both invaded by *P. arundinacea*, but occur on different soil types having distinctly different hydroperiods; therefore, communities C and D were compared to assess the effect of soil type and hydroperiod on carbon storage.

Table 1. Descriptive summary of plant communities. Summary of vegetation cover, hydrology, and soils within each study plot at Beanblossom Bottoms. Plant community A was used as a reference plot to make general comparisons with the other communities. Plant communities B and C were used to compare the effect of different species on carbon sequestration because both communities occur on the same soil and experience the same wetland hydroperiod. Plots C and D were used to compare the effect of different wetland hydroperiods and soil types on carbon sequestration because *P. arundinacea*, inhabits both plots.

Plot #	Plant Community	Plan of Analyses		Description
2	A	Mixed Native, Reference Plot		• Mixed native assemblage of 24 species; *Carex lurida* (14.2%), *Juncus effusus* (12.6%), *Solidago canadensis* (12.6%), and *Juncus interior* (12.1%) all having co-dominance. Seasonally saturated. Soil series: Stendal; somewhat poorly drained silt loam, Inceptisols.
4	B		Effect of Vegetation	• *Scirpus cyperinus* (74%) dominated stand with 25% *Juncus effusus*. Variably flooded with deep (> 50 cm) water. Soil series: Zipp; poorly drained silty clay loam, Inceptisols.
3	C	Effect of Hydroperiod		• Monotypic stands of *P. arundinacea* (100%). Variably flooded with deep (> 50 cm) water. Soil series: Zipp; poorly drained silty clay loam, Inceptisols.
1	D			• Nearly monotypic stands of *P. arundinacea* (92%). Seasonally ponded. Soil series: Bonnie; poorly drained silt loam, Entisols.

Table 2. Vegetation cover – Plant community A. *Carex lurida, Juncus effusus, Solidago canadensis*, and *Juncus interior* were co-dominants in this plot.

Mixed native assemblage				
Species		**% Relative**	**Wetland indicator**	**Plant**
Scientific name	**Common name**	**Over**	**status**	**type**
Carex lurida	Shallow sedge	14.2	OBL	monocotyledon
Juncus effusus	Soft rush	12.6	OBL	monocotyledon
Solidago canadensis	Canada goldenrod	12.6	FACU	dicotyledon
Juncus interior	Inland rush	12.1	FAC+	monocotyledon
Galium triflorum	Fragrant bedstraw	8.4	FACU+	dicotyledon
Solidago lancifolia	Lance leaf goldenrod	6.4	NI	dicotyledon
Agrimonia sp.	Agrimony	6.2	FACU	dicotyledon
Verbena hastate	Swamp verbena	5.2	FACW+	dicotyledon
Polygonum sagittatum	Arrowleaf tearthumb	3.0	OBL	dicotyledon
Eupatorium perfoliatum	Boneset	3.0	FACW+	dicotyledon
Carex vulpinoidea	Fox sedge	2.4	OBL	monocotyledon
Geum laciniatum	Rough avens	2.2	FACW	dicotyledon
Unid. aster 1	Unid. aster 1	2.2	NI	dicotyledon
Galium obtusum	Bluntleaf bedstraw	1.8	FACW+	dicotyledon
Unid. aster 2	Unid. aster 2.	1.6	NI	dicotyledon
Carex bebbii	Bebb's sedge	1.6	OBL	monocotyledon
Impatiens parviflora	Touch me not	1.2	NI	dicotyledon
Onoclea sensibilis	Sensitive fern	0.8	FACW	fern
Ludwigia alternifolia	Seedbox	0.6	OBL	dicotyledon
Scirpus atrovirens	Dark green bulrush	0.6	OBL	monocotyledon
Unid. aster 3	Unid. aster 3	0.5	NI	dicotyledon
Epilobium sp.	Willowherb	0.4	OBL	dicotyledon
Leersia oryzoides	Rice cutgrass	0.2	OBL	monocotyledon
Acer rubrum	Red maple	0.2	FAC	dicotyledon

Table 3.Vegetation cover – Plant community B. *Scirpus cyperinus* and *Juncus effusus* dominated this plot.

***Scirpus cyperinus*/*Juncus effusus* dominated plot**				
Species		**% relative**	**wetland indicator**	**plant**
Scientific name	**Common name**	**Cover**	**Status**	**type**
Scirpus cyperinus	Wool grass	74.0	OBL	monocotyledon
Juncus effusus	Soft rush	24.6	OBL	monocotyledon
Leersia oryzoides	Rice cut grass	0.4	OBL	monocotyledon
Galium sp.	Bedstraw species	0.4	FAC	dicotyledon
Carex bebbii	Bebb's sedge	0.4	OBL	monocotyledon
Bidens pilosa	Hairy beggarticks	0.1	NI	dicotyledon

Figure 9. Vegetation cover – Plant community C. The area invaded did not encompass a complete 10 m radius plot; therefore, three quadrats (100% *P. arundinacea*) were established for vegetation and soil sampling within the outlined region.

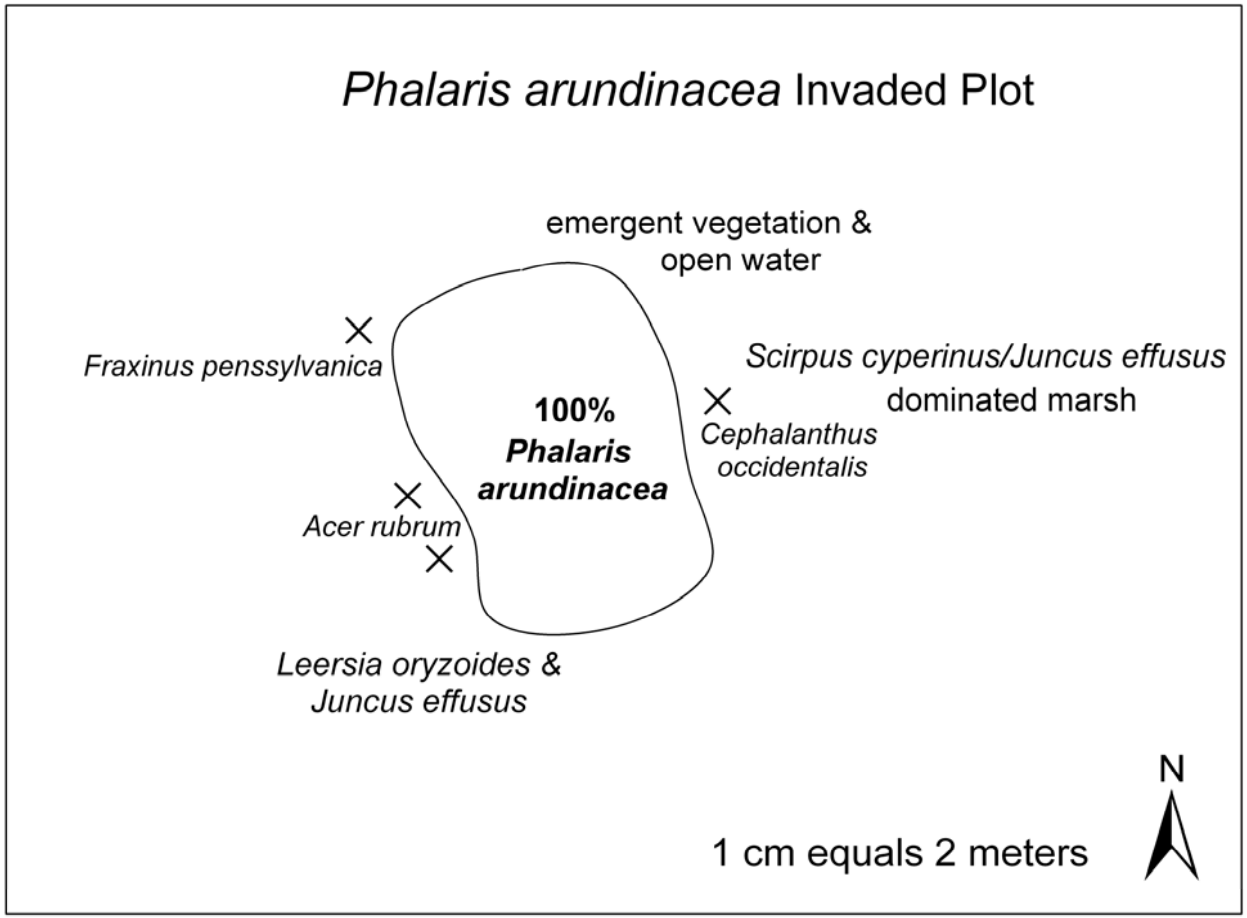


Table 4. Vegetation cover – Plant community D. *P. arundinacea* dominated plot.

***P. arundinacea* invaded plot**				
Species		**% relative**	**Wetland indicator**	**plant**
Scientific name	**Common name**	**Cover**	**Status**	**type**
Phalaris arundinacea	Reed canary grass	91.9	FACW+	monocotyledon
Carex vulpinoidea	Fox sedge	3.5	OBL	monocotyledon
Onoclea sensibilis	Sensitive fern	1.9	FACW	fern
Galium obtusum	Bluntleaf bedstraw	1.4	FACW+	dicotyledon
Carex sp.	Sedge species	0.4	FACW	monocotyledon
Agrimonia sp.	Agrimony	0.4	FACU	dicotyledon
Scirpus cyperinus	Wool grass	0.4	OBL	monocotyledon
Epilobium sp.	Willowherb	0.1	OBL	dicotyledon
Geum sp.	Avens	0.1	FAC	dicotyledon

Using the methodology proposed by Tiner (1999), a prevalence index was computed for each of the vegetation communities at the study site. Communities A, B, and D scored 2.35, 1 and 2 on the scale. A prevalence index was not calculated for native plant community C because relative percent cover was not recorded; however, since *P. arundinacea* is a facultative wetland plant (FACW), a rating of 2 was assigned (similar to the other *P. arundinacea* dominated community). Using these index values, a hierarchy of hydrologic regimes can be established for the study plots at Beanblossom Bottoms: Plot A < Plot C = Plot D < Plot B; with Plot B being the wettest plot. Ninety-nine percent of the vegetation in plot B (Table 3) consisted of two obligate wetland species, confirming that only a few species are capable of tolerating deep (> 50 cm) water conditions during the growing season.

Soil Physiochemical Properties

Soils at the study site were generally similar in terms of their major physiochemical characteristics (Table 5). Soil pH across all plots and all depths averaged 5.3 with a maximum of 6.18 and a minimum of 4.73 (Table 5). Thus, given the acidity of the soils, it was concluded that carbonates would constitute a negligible soil carbon pool at the study site. Therefore, soil samples were not tested for carbonates.

Averaged across plots and depths, clay, silt, and sand concentrations averaged 39%, 34%, and 27%, respectively (Table 5). It was also noted that plant communities B and C occur within the poorly-drained Zipp soil series which contain 5% more clay than soils at the other communities.

At field capacity, soils from communities A and B contained on average 36.73 and 38.1 grams H_2O per 100 grams soil, respectively. These results are consistent with the observation that soils in Plot B contain 5% more clay than soils in Plot A. In addition, hydrograph data showed that water ponded at the surface for longer time periods in Plot B than in Plot A.

Bulk density ranged from 1.05 to 1.51 g cm^{-3} and exhibited a gradual increase with soil depth (Table 5). Statistically significant ($P < 0.05$) differences in bulk density among plots were detected in the 5-10 cm and 10-15 cm depth intervals.

Table 5. Soil physiochemical properties. A record of physiochemical properties of the soils sampled at Beanblossom Bottoms. Plus or minus values represent one standard deviation from the mean (n = 3).

Plant community	Depth (cm)	Bulk density G cm^{-3}	pH	% Sand	% Silt	% Clay
A[†]	0-5	1.09 ± 0.06	5.10 ± 0.26	26 ± 1	37 ± 1	37 ± 3
	5-10	1.15 ± 0.08	5.12 ± 0.20	29 ± 4	37 ± 4	34 ± 4
	10-15	1.27 ± 0.06	5.17 ± 0.18	25 ± 6	38 ± 6	37 ± 4
	15-30	1.38 ± 0.01	5.17 ± 0.31	26 ± 1	37 ± 1	37 ± 1
B	0-5	1.11 ± 0.15	4.73 ± 0.11	24 ± 2	32 ± 2	44 ± 2
	5-10	1.30 ± 0.11	4.87 ± 0.19	24 ± 4	34 ± 4	42 ± 5
	10-15	1.33 ± 0.02	5.53 ± 0.16	33 ± 1	28 ± 1	39 ± 7
	15-30	1.36 ± 0.02	6.18 ± 0.22	26 ± 2	32 ± 2	42 ± 0
C	0-5	1.19 ± 0.16	4.96 ± 0.26	27 ± 1	33 ± 1	40 ± 2
	5-10	1.37 ± 0.01	5.22 ± 0.25	30 ± 2	33 ± 2	37 ± 10
	10-15	1.50 ± 0.07	5.55 ± 0.54	25 ± 3	32 ± 3	43 ± 3
	15-30	1.51 ± 0.10	6.17 ± 0.27	30 ± 3	30 ± 3	39 ± 3
D	0-5	1.05 ± 0.17	5.00 ± 0.25	26 ± 1	35 ± 1	39 ± 1
	5-10	1.26 ± 0.07	5.21 ± 0.16	22 ± 2	35 ± 2	42 ± 12
	10-15	1.36 ± 0.02	5.55 ± 0.10	27 ± 2	37 ± 2	36 ± 7
	15-30	1.40 ± 0.06	5.62 ± 0.21	26 ± 1	35 ± 1	39 ± 2

[†]Plant community A represents a seasonally saturated mixed native reference plot, B a variably flooded *Scirpus cyperinus* dominated plot, C a variably flooded *P. arundinacea* invaded plot, and D a seasonally ponded *P. arundinacea* invaded plot.

Primary Productivity

Above-Ground Biomass

Above-ground biomass data (Table 6) were analyzed using ANOVA with season and species as class variables. This analysis showed a statistically significant ($P < 0.0001$) effect of species with respect to biomass production. Post hoc t-tests showed that *S. cyperinus* generated greater quantities of above-ground biomass than any of the other species. Averaged across sampling occasions and community quadrats, mean above-ground biomass production of *S. cyperinus* was 1835 g m^{-2}. This amount was 2-3 times the average production of the other species sampled (mean: 732 g m^{-2}). No difference in above-ground biomass production was detected among the other plant communities sampled. Above-ground biomass input from *P. arundinacea* averaged 693 g m^{-2} across both sampling occasions and plant communities C and D. Mixed native species averaged 810 g m^{-2} above-ground biomass (Table 6, Fig. 10). ANOVA also revealed a significant effect of season ($P < 0.001$) with more biomass collected in the middle of the growing season (July) than at the end of the growing season (October) (Fig. 10, Table 6). However, this level of significance is more heavily weighted on the growth pattern of *Scirpus cyperinus* (Plot B) than any of the other plant communities (Table 6).

Table 6. Above-ground biomass. Masses of oven dry above-ground biomass collected from Beanblossom Bottoms during the growing season. One sampling occurred in July (middle-of-season) and the other occurred in October (end-of-season) 2007. Averages are representative of three quadrats; ± values represent one standard deviation from the mean. Within a column, means followed by different letters (capitals or lower case) are significantly different at the 0.05 probability level. Capital letters represent the comparison between the variably flooded *S. cyperinus* dominated plant community and the variably flooded *P. arundinacea* monoculture. Lower case letters represent the comparison between the two *P. arundinacea* invaded plant communities having two different hydroperiods.

Above-ground biomass collected during the growing season						
Plant community	Middle-of-season		End-of-season		Averaged for entire season	
	avg.	±	avg.	±	avg.	±
	G m^{-2}		g m^{-2}		g m^{-2}	
A[†]	839	77	780	173	810	42
B[‡]	2156A	373	1531A	25	1835A	365
C	884Ba	43	659Ba	141	772Ba	159
D	690a	14	536a	51	613a	109

[†]Plant community A represents a seasonally saturated mixed native reference plot, B a variably flooded *S. cyperinus* dominated plot, C a variably flooded *P. arundinacea* monoculture, and D a seasonally ponded *P. arundinacea* dominated plot.
[‡]Only two quadrats of *S. cyperinus* were sampled in plant community B.

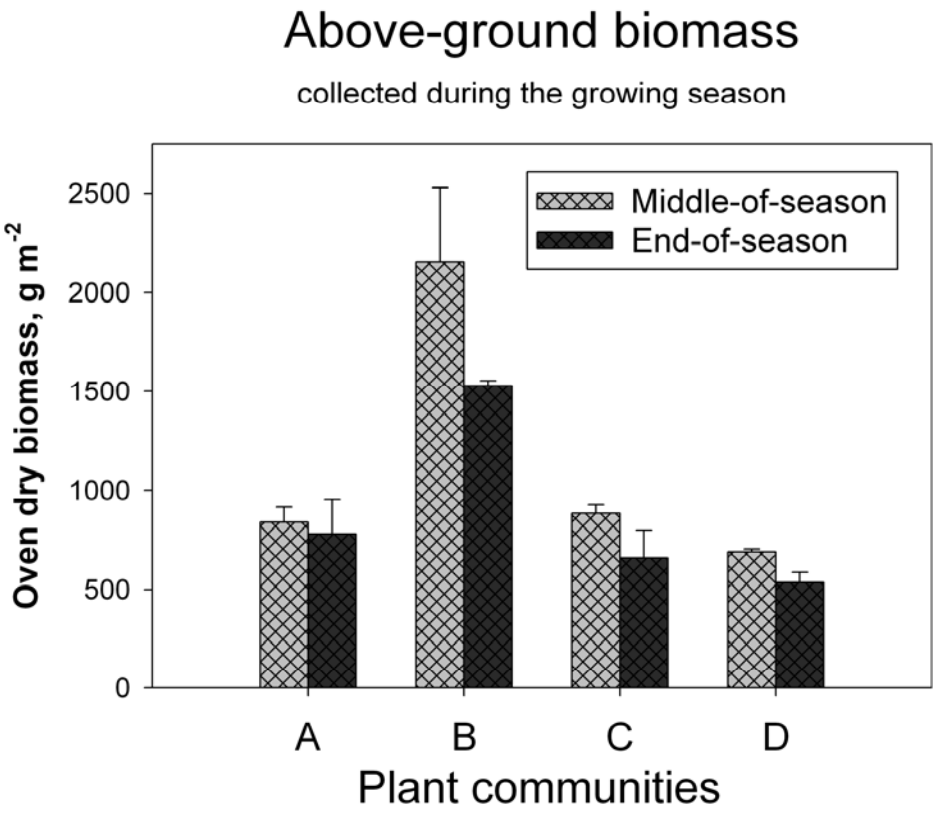


Figure 10. Above-ground biomass. Above-ground biomass as related to plant community and sampling occasion within the growing season. The middle of season sampling occurred in July 2007, and the end of season sampling took place in October 2007. Plant community A consisted of a mixed native assemblage, community B consisted of 2 quadrats of *S. cyperinus*, community C consisted of a variably flooded *P. arundinacea* monoculture, and community D consisted of a seasonally ponded *P. arundinacea* dominated plot.

Below-ground Biomass

As with above-ground biomass, root biomass data (Table 7) were subjected to ANOVA to test for the effect of sampling occasion and plant species. In this analysis, data for each depth interval was analyzed separately. At any of the soil depths sampled, ANOVA showed no significant ($P > 0.05$) effect of either season or plant species on root biomass distribution. The lack of significant differences was probably due to the high variability among plant community replicates (Table 7). Numerically nonetheless, *S. cyperinus* appears somewhat different among the plant species with an overall greater root biomass and an increase in the mass of roots collected (0-5 cm layer) between the middle to late season samplings. Across sampling occasions, total root mass collected in the 0-30 cm soil layer averaged 179, 237, and 309 g biomass m^{-2} in the mixed native, *P. arundinacea* and *S. cyperinus* vegetation communities, respectively.

Table 7. Below-ground biomass. Values are means with standard deviations in parentheses (n = 3). Plant communities consisted of the following: A, a seasonally saturated mixed native reference plot; B, a variably flooded *S. cyperinus* dominated plot; C, a variably flooded *P. arundinacea* invaded plot; D, a seasonally ponded *P. arundinacea* invaded plot.

Below-ground biomass								
		root mass, g m^{-2}						
Plant community	depth (cm)	Middle-of-season		End-of-season		Averaged for entire season		
A	0-5	180	(24)	122	(79)	151	(38)	
	5-10	29	(14)	9	(4)	19	(9)	
	10-15	7	(4)	3	(0)	5	(2)	
	15-30	7	(4)	1	(1)	4	(2)	
B[†]	0-5	175	(177)	371	(129)	263	(24)	
	5-10	32	(15)	31	(12)	26	(10)	
	10-15	7	(1)	10	(11)	10	(4)	
	15-30	9	(0)	15	(9)	10	(5)	
C	0-5	259	(69)	95	(15)	177	(29)	
	5-10	20	(1)	10	(7)	15	(4)	
	10-15	5	(3)	4	(3)	5	(2)	
	15-30	13	(12)	4	(1)	9	(6)	
D	0-5	184	(30)	171	(90)	178	(55)	
	5-10	69	(24)	55	(21)	62	(22)	
	10-15	18	(1)	9	(5)	13	(3)	
	15-30	20	(7)	9	(5)	15	(3)	

[†]This particular sampling set consisted of only two cores instead of 3 (n = 2).

Soil Organic Carbon

In the top 5 cm soil interval, soil C concentration (g C kg^{-1} soil) averaged 9.65 in the seasonally saturated mixed native plot (plant community A), 14.33 in the variably flooded *S. cyperinus* dominated plot (plant community B), 13.38 in the variably flooded *P. arundinacea* invaded plot (plant community C), and 17.22 in the seasonally ponded *P. arundinacea* invaded plot (plant community D) (Table 8). Total organic carbon pools (0-30 cm) (Fig. 11) ranged from 18.7 Mg C ha^{-1} in the saturated mixed native plot (A) to 25.5 Mg C ha^{-1} in the variably flooded *P. arundinacea* plot (C).

Soil organic carbon (SOC) under plant communities B and C were compared using a paired t-test to determine the effect of species on carbon storage. Results showed that the area invaded by *P. arundinacea* in plant community C had significantly ($P < 0.05$) greater SOC content in the 5-10 cm soil layer compared to areas dominated by *S. cyperinus* (community B) (Fig. 12). However, there was no significant ($P > 0.05$) difference in SOC stocks between the two *P. arundinacea* invaded plots experiencing two distinct hydroperiods (communities C and D). Thus, it appears that SOC storage in areas invaded by *P. arundinacea* is not significantly influenced by hydroperiod.

Table 8. Soil organic carbon (SOC). Soil organic carbon concentration (g C kg^{-1} soil) as related to vegetation and hydrology at Beanblossom Bottoms, a wetland complex in south – central Indiana. Data are means with standard deviations in parentheses. Plant communities B and C were used to compare the effect of vegetation type on the size of carbon stocks while plant communities C and D were used to compare the effect of hydrology on carbon storage.

	Seasonally saturated	Variably flooded with deep (> 50 cm) water		Seasonally ponded
			__ Effect of hydroperiod __	
Soil depth, cm	Mixed native plants (A)	_____ Effect of vegetation _____ *S. cyperinus* (B)	*P. arundinacea* (C)	*P. arundinacea* (D)
0 – 5	9.65 (2.38)	14.33 (2.3)	13.38 (2.32)	17.22 (4.04)
5 – 10	6.85 (1.2)	6.68 (1.11)	8.58 (0.73)	8.09 (1.99)
10 – 15	5.36 (0.58)	5.9 (1.4)	7 (1.11)	5.76 (0.81)
15 – 30	4.45 (0.75)	3.6 (1.3)	4.7 (0.94)	4.12 (1)

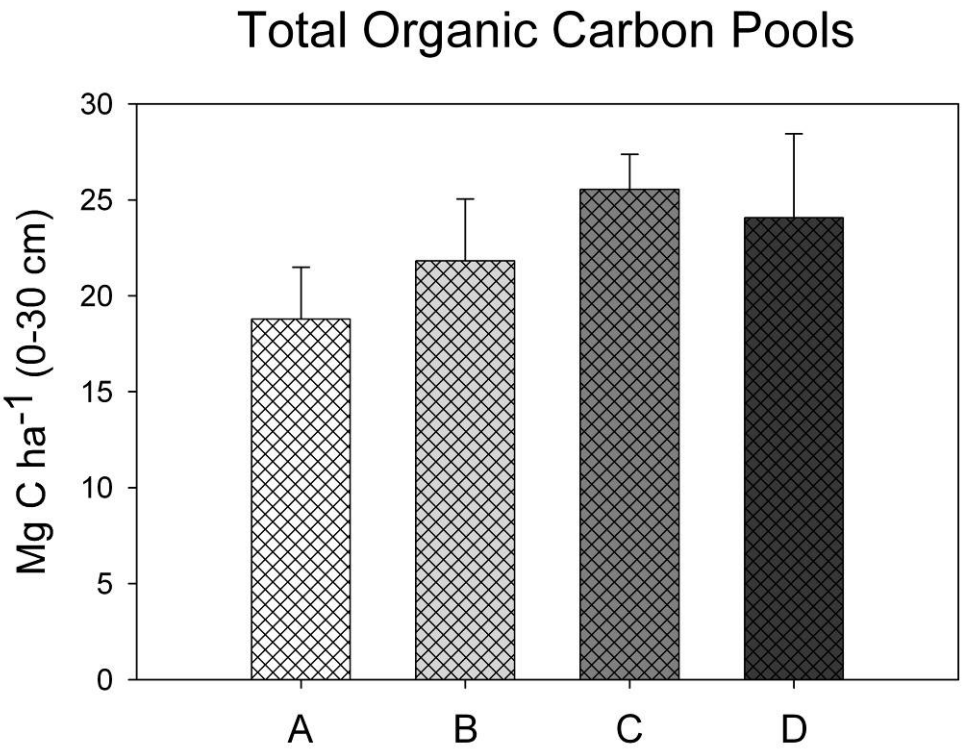


Figure 11. Total organic carbon pools. Letters represent plant communities; community A was a seasonally saturated mixed stand of 24 native species, community B was a variably flooded stand of native species dominated by *S. cyperinus*, community C consisted of a variably flooded monoculture of *P. arundinacea*, and community D consisted of a seasonally ponded stand dominated by *P. arundinacea.* All plant communities had n = 6 replicates except plant community B which is reported as n = 4 replicates under *S. cyperinus* plants.

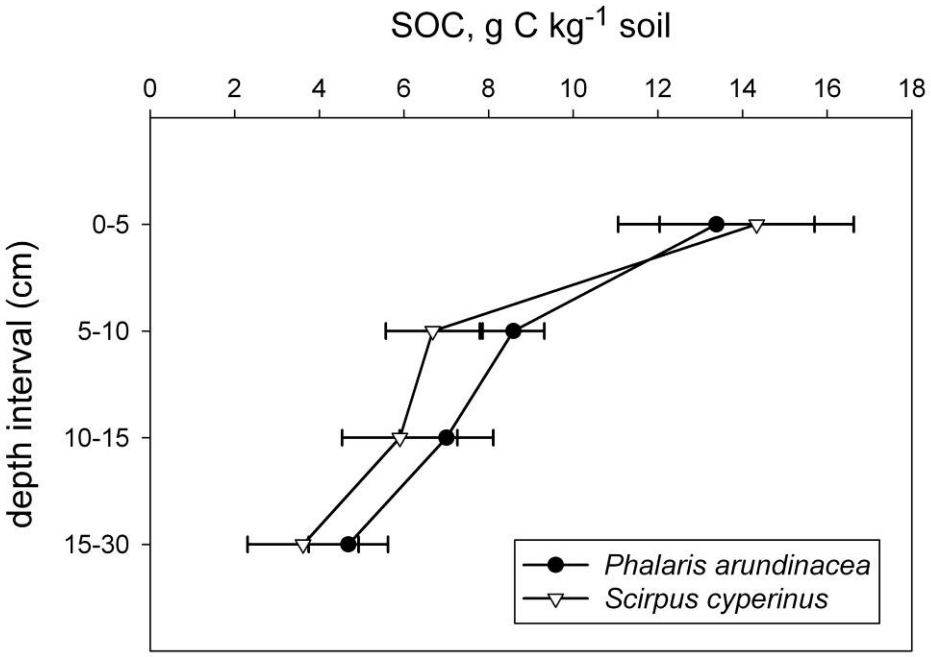


Figure 12. Depth distribution of SOC under *S. cyperinus* and *P. arundinacea*. Depth distribution of soil organic carbon (SOC) under *S. cyperinus* in plant community B and *P. arundinacea* in plant community C. The *P. arundinacea* invaded plot contained n = 6 replicates and the *S. cyperinus* dominated plot contained n = 4 replicates.

Soil Nitrogen

Average values for soil organic nitrogen concentration ranged from 0.85 to 1.82 g N kg^{-1} soil in the top 5 cm (Table 9). No significant ($P > 0.05$) differences were found among plant communities for any depth but the 0-5 cm interval. There was no significant ($P > 0.05$) difference in nitrogen concentration between *P. arundinacea* invaded plant communities as related to hydrology. Soil organic nitrogen was significantly ($P < 0.05$) greater under *P. arundinacea* (communities C and D) than under the mixed native assemblage (community A). There was no significant difference ($P > 0.05$) between pools of nitrogen under *S. cyperinus* (community B) and *P. arundinacea* (community C) (Table 9).

Table 9. Soil nitrogen. Soil nitrogen concentration (g N kg^{-1} soil) as related to vegetation and hydrology in a wetland complex in south – central Indiana. Data are means with standard deviations in parentheses. Plant communities B and C were used to compare the effect of vegetation; whereas plant communities C and D were used to compare the effect of different hydroperiods on soil nitrogen concentration at the study site. Communities A and D were compared to represent the effects of a mixed native plot and a *P. arundinacea* invaded community on soil organic nitrogen pools.

	Seasonally saturated	Variably flooded with deep (> 50 cm) water		Seasonally ponded
			__ Effect of different hydroperiods __	
		_____ Effect of vegetation _____		
Soil depth, cm	Mixed native plants (A)	*S. cyperinus* (B)	*P. arundinacea* (C)	*P. arundinacea* (D)
0 - 5	0.85 (0.39)	1.42 (0.14)	1.49 (0.17)	1.82 (0.32)
5 - 10	0.67 (0.38)	0.88 (0.13)	1.12 (0.22)	1.04 (0.18)
10 - 15	0.58 (0.34)	0.79 (0.19)	0.97 (0.21)	0.84 (0.15)
15 - 30	0.50 (0.37)	0.65 (0.25)	0.77 (0.24)	0.69 (0.24)

Biochemistry of Biomass

Maximum and minimum concentrations of biochemical constituents grouped for all vegetation communities and sampling occasions ranged as follows: carbon, 115 to 379 g kg^{-1}; nitrogen, 4.4 to 15.1 g kg^{-1}; cellulose, 64 to 288 g kg^{-1}; lignin, 65 to 181 g kg^{-1}; phenolics, 3 to 39 g kg^{-1}; acid detergent fiber, 363 to 769 g kg^{-1} (Table 10). Statistical analyses showed no significant effect of hydroperiod on any of the residue quality parameters (Table 11). For most parameters, statistically significant differences in biomass quality were found among species and between above and below-ground biomass (Tables 11 and 12).

P. arundinacea above-ground biomass contained less phenolics (mean: 10 g kg^{-1} biomass) (Table 10) than the other wetland plant species (33 and 37 g kg^{-1} biomass for the mixed natives and *S. cyperinus,* respectively) (Fig. 13). The composition of the below-ground biomass followed a similar pattern (Fig. 14). C to N ratios of *P. arundinacea* biomass were also lower (C/N:19) than those of native species (mean C/N: 33).

Overall, biomass collected at the end of the growing season contained significantly ($P < 0.0001$) more lignin in their roots than in their shoots (Table 10). However, analysis of the biomass collected in the middle of the growing season showed variation among vegetation communities with respect to lignin allocation; in the mixed native assemblage, more lignin was allocated to above-ground biomass, whereas in the communities dominated by *S. cyperinus* (B) and *P. arundinacea* (C and D) more lignin was allocated to below-ground biomass (Table 10, Figs. 15 and 16). Among above-ground biomass samples collected at the end of the growing

season, lignin concentration was greater in the mixed native and *S. Cyperinus* dominated community (154 g kg^{-1}) than in the *P. arundinacea* invaded communities (70.5 g kg^{-1}). A similar trend was observed with below-ground biomass (Table 10). *P. arundinacea* biomass collected from community C (variably flooded) generally had much lower Lignin:N ratios, compared to biomass collected from the other communities including *P. arundinacea* collected from plot D (seasonally ponded) (Table 10, Figs. 17 and 18). This pattern was consistent for both samplings during the growing season.

Table 10. Biomass biochemistry. Biochemical composition of above and below-ground biomass collected from vegetation communities during the middle and end of the growing season. Plant communities were as follows: community A was a mixed stand of 24 native species, community B was dominated by *S. cyperinus*, community C consisted of a monoculture of *P. arundinacea*, and community D was dominated *P. arundinacea*. Values are means with standard deviations in parentheses.

	Cellulose	Lignin	Phenolics	Carbon	Nitrogen	Acid det. Fiber	C : N	Lignin : N
Plant Community	g kg^{-1}							
***Above-ground* biomass Middle-of-season**								
A	179 (53)	110 (17)	33 (4)	283 (55)	8.5 (1.0)	443 (8)	33 (3)	13.2 (3.7)
B	233 (9)	135 (27)	37 (5)	379 (11)	12.4 (2.6)	415 (6)	31 (6)	10.8 (0.8)
C	201 (38)	77 (8)	9 (3)	325 (50)	15.1 (0.7)	379 (4)	21 (2)	5.1 (0.7)
D	172 (22)	70 (6)	12 (5)	265 (16)	13.7 (0.8)	411 (4)	19 (1)	5.1 (0.4)
Below-ground biomass Middle-of-season								
A	64 (32)	83 (32)	12 (3)	127 (69)	4.4 (1.4)	769 (10)	27 (6)	18.4 (1.3)
B	163 (63)	168 (22)	19 (8)	272 (81)	8.6 (0.8)	594 (6)	32 (9)	19.5 (1.0)
C	86 (30)	98 (14)	3 (1)	189 (38)	10.1 (1.2)	645 (5)	19 (2)	9.7 (0.2)
D	128 (51)	88 (26)	3 (1)	115 (5)	4.6 (0.5)	564 (9)	25 (2)	18.9 (4.3)
***Above-ground* biomass End-of-season**								
A	249 (46)	158 (14)	23 (5)	196 (33)	5.7 (0.4)	500 (3)	34 (3)	27.8 (4.7)
B	288 (13)	150 (46)	21 (2)	200 (24)	8.6 (1.3)	473 (14)	23 (1)	17.6 (0.7)
C	170 (16)	76 (17)	16 (4)	221 (18)	13.7 (0.5)	363 (3)	16 (1)	5.6 (1.5)
D	116 (63)	65 (10)	8 (3)	137 (67)	7.0 (3.2)	594 (16)	20 (1)	10.3 (3.4)
Below-ground biomass End-of-season								
A	198 (11)	175 (17)	34 (16)	205 (17)	9.3 (4.1)	458 (3)	25 (9)	21.8 (10.7)
B	196 (24)	181 (34)	39 (17)	206 (29)	8.7 (1.3)	503 (4)	24 (0)	20.9 (1.5)
C	192 (15)	115 (14)	7 (3)	169 (7)	7.6 (0.5)	453 (1)	22 (2)	15.2 (2.0)
D	174 (28)	109 (17)	4 (1)	148 (51)	5.5 (1.5)	435 (7)	27 (3)	20.2 (2.6)

Table 11. Summary of ANOVA analysis – Biomass biochemistry. (a) Above-ground biomass, and (b) Below-ground biomass. Analysis was conducted for each season separately.

(a) Above-ground biomass

Factors	Cellulose		Lignin		Phenolics		Lignin : N	
Season	Middle	End	Middle	End	Middle	End	Middle	End
hydrology	NS	NS	NS	NS	NS	NS	NS	NS
Species	NS	*	**	***	***	*	**	***
hydrology x Species	NS	NS	NS	NS	NS	NS	NS	NS

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.

(b) Below-ground biomass

Factors	Cellulose		Lignin		Phenolics		Lignin : N	
Season	Middle	End	Middle	End	Middle	End	Middle	End
hydrology	NS	NS	NS	NS	NS	NS	NS	NS
Species	NS	NS	*	**	**	**	**	NS
hydrology x Species	NS	NS	NS	NS	NS	NS	NS	NS

Table 12. Summary of ANOVA analysis – Above and below-ground biomass biochemistry. AG and BG are abbreviations representing above-ground and below-ground biomass.

Factors	Lignin		Cellulose		Phenolics		C		N		C : N		Lignin : N	
Season	Middle	End	Middle	End	Middle	End	Middle	End	Middle	End	Middle	End	Middle	End
AG vs BG	NS	***	***	NS	***	NS	***	NS	**	NS	NS	NS	***	*
Species	***	***	*	*	***	***	*	NS	*	NS	**	*	*	**

* Significant at the 0.05 probability level.
** Significant at the 0.001 probability level.
*** Significant at the 0.0001 probability level.

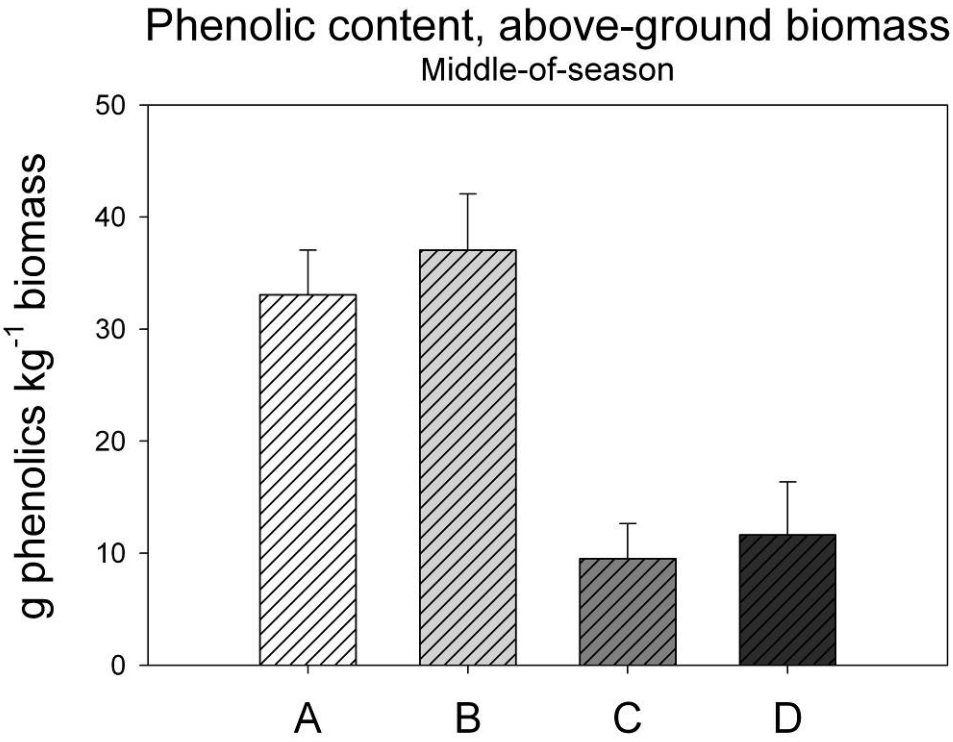


Figure 13. Phenolic content – Above-ground biomass. Letters represent plant communities; community A was a mixed stand of 24 native species, community B was dominated by *S. cyperinus*, community C consisted of a monoculture of *P. arundinacea*, and community D was a *P. arundinacea* dominated plot.

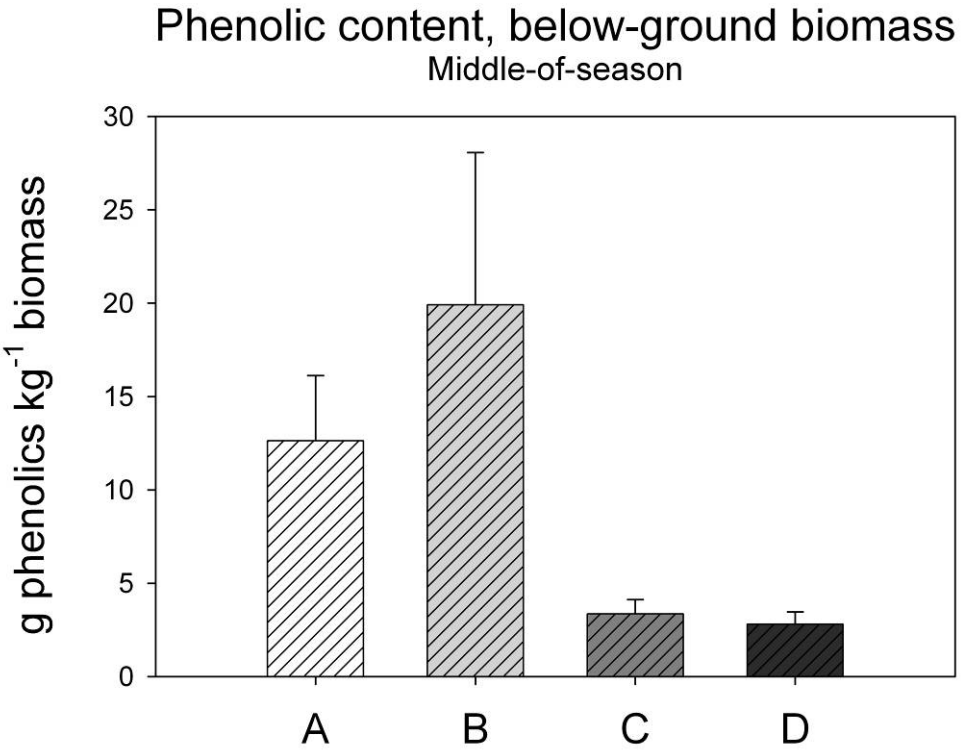


Figure 14. Phenolic content – Below-ground biomass. Letters represent plant communities; community A was a mixed stand of 24 native species, community B was dominated by *S. cyperinus*, community C consisted of a monoculture of *P. arundinacea*, and community D was a *P. arundinacea* dominated plot.

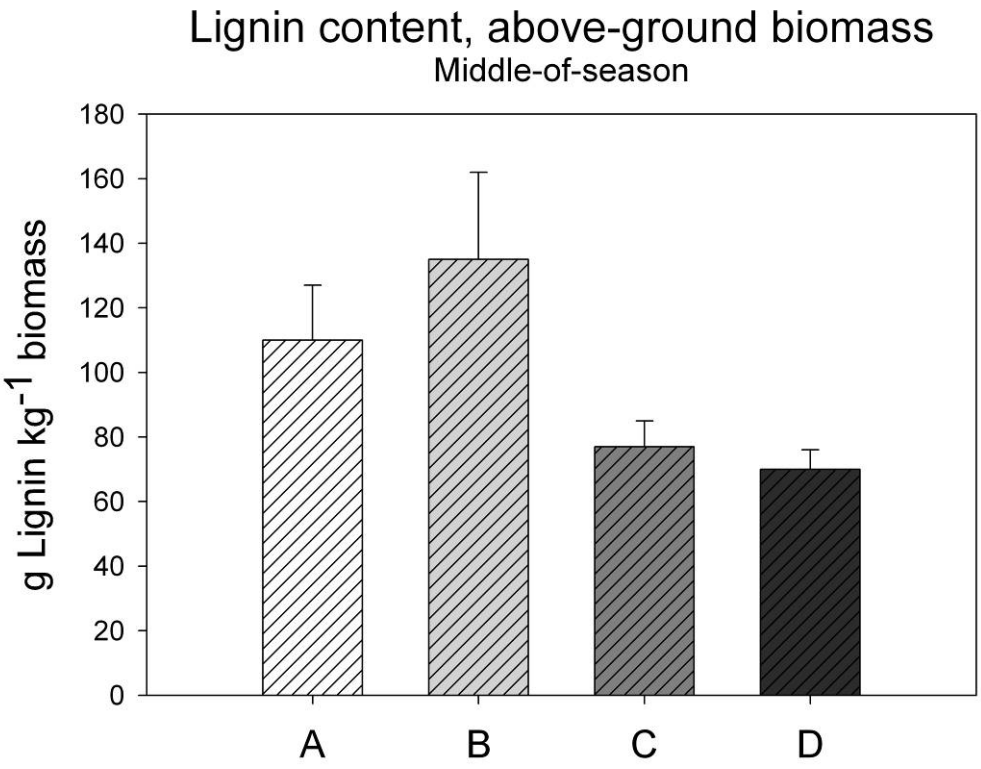


Figure 15. Lignin content – Above-ground biomass. Letters represent plant communities; community A was a mixed stand of 24 native species, community B was dominated by *S. cyperinus*, community C consisted of a monoculture of *P. arundinacea*, and community D was a *P. arundinacea* dominated plot.

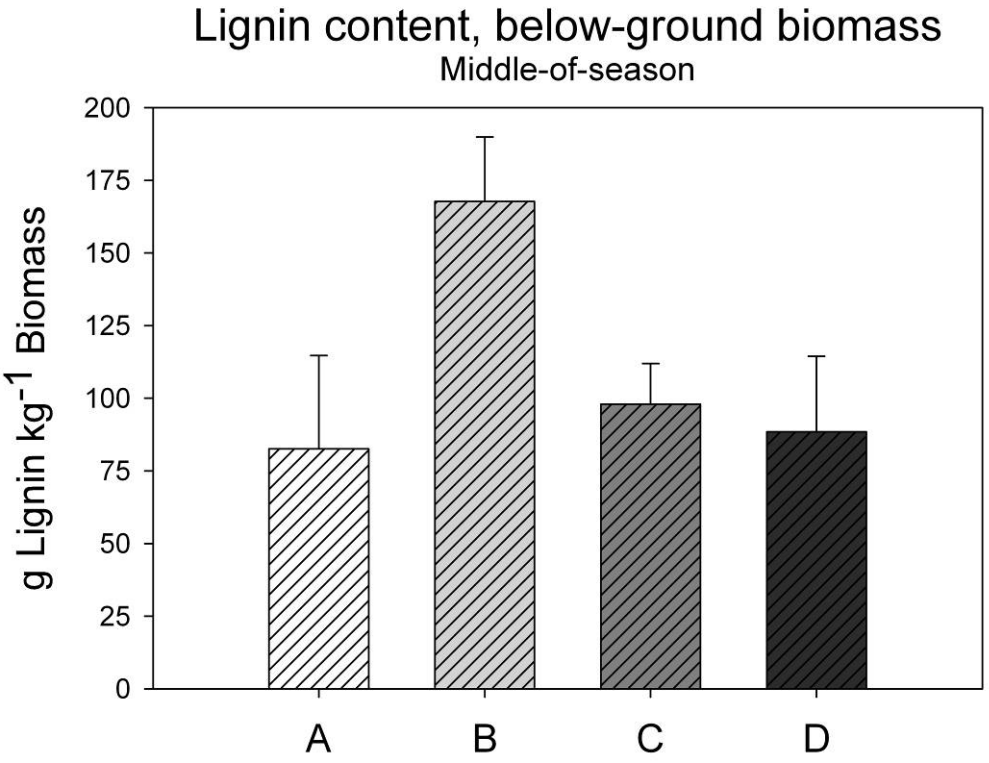


Figure 16. Lignin content – Below-ground biomass. Letters represent plant communities; community A was a mixed stand of 24 native species, community B was dominated by *S. cyperinus*, community C consisted of a monoculture of *P. arundinacea*, and community D was a *P. arundinacea* dominated plot.

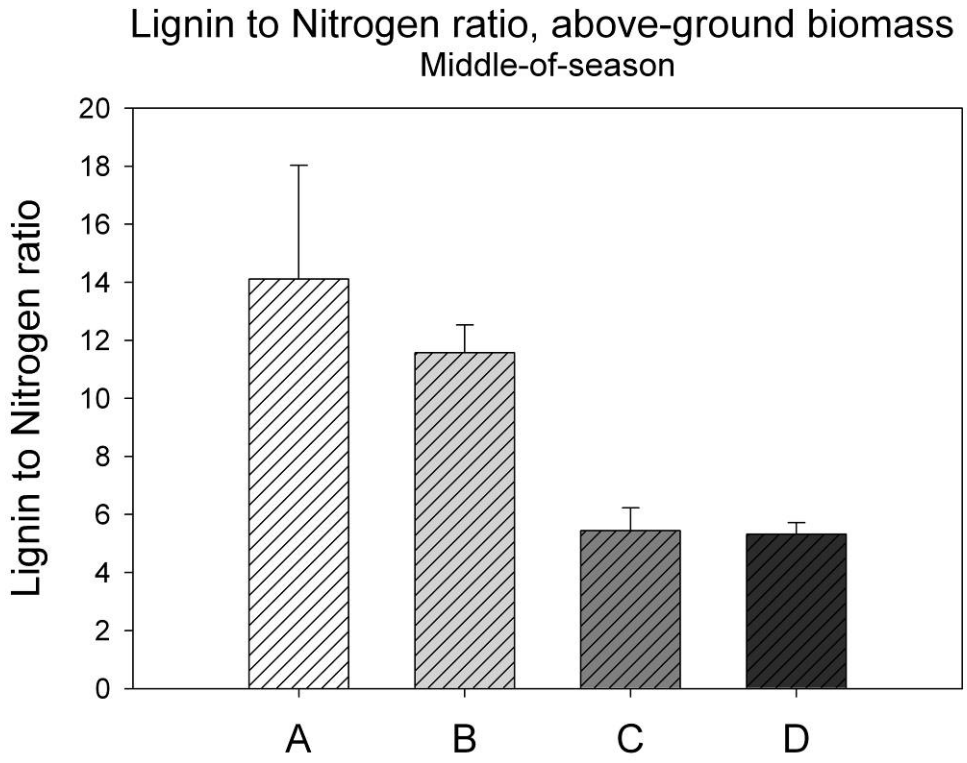


Figure 17. Lignin to nitrogen ratio – Above-ground biomass. Letters represent plant communities; community A was a mixed stand of 24 native species, community B was dominated by *S. cyperinus*, community C consisted of a monoculture of *P. arundinacea*, and community D was a *P. arundinacea* dominated plot.

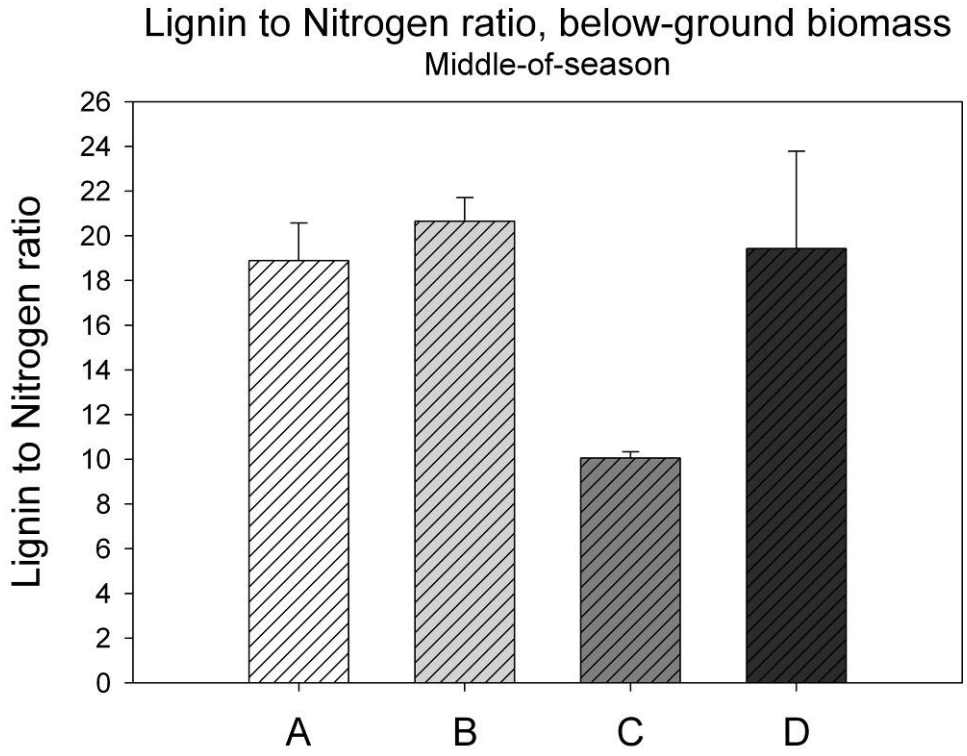


Figure 18. Lignin to nitrogen ratio – Below-ground biomass. Letters represent plant communities; community A was a mixed stand of 24 native species, community B was dominated by *S. cyperinus*, community C consisted of a monoculture of *P. arundinacea*, and community D was a *P. arundinacea* dominated plot.

Decomposition Study

Various sections of the wetland complex have experienced *P. arundinacea* invasion in recent years. As outlined in Table 1, communities A and B represent native vegetation communities that could potentially become invaded by *P. arundinacea.* As stated in one of the study hypotheses and suggested by the residue quality data (Tables 10, 11, and 12), invasion by *P. arundinacea* could alter C dynamics in wetland soils. With these considerations in mind, a decomposition study of *P. arundinacea* biomass was conducted with soils from adjacent plots supporting native vegetation communities. Thus, *P. arundinacea* biomass from community D was incubated in soils from community A. Likewise, *P. arundinacea* biomass from community C was incubated in soils from community B. Biomass from native communities (A and B) were incubated in their respective soil types.

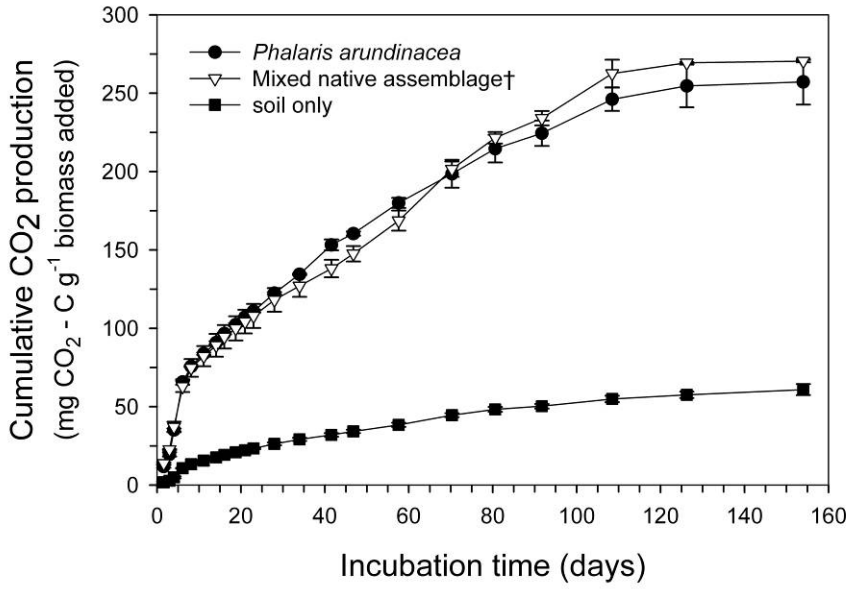
During a 154 day incubation study, the amount of CO_2-C released from soils collected from native plant communities A and B averaged 61 ± 4 and 21 ± 7 mg CO_2-C kg^{-1}, respectively. These results suggest that microbial activity in these two soils may be different. Therefore, results of the decomposition study are described separately for each of these two soils. Biochemical composition of the biomass (above and below-ground) used in the incubation study is given in Table 10.

In soils collected from community A, above-ground biomass of *P. arundinacea* and the mixed native species decomposed at similar rates. At the end of the incubation period (154 days) the amounts of C released as CO_2 was 257 and 270 mg CO_2-C, from *P. arundinacea* and the mixed native species, respectively (Table 13, Fig. 19a). Decomposition of below-ground biomass was less rapid, but, once

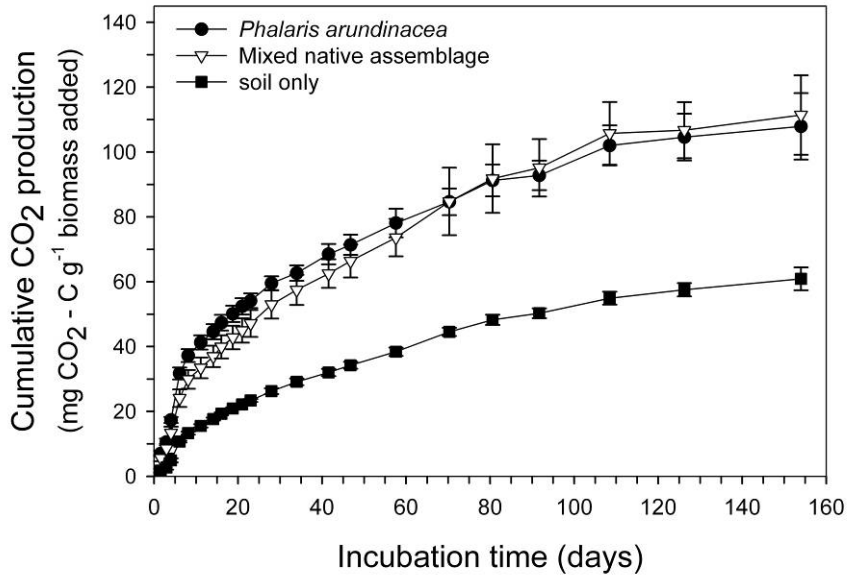
again, both species decomposed at similar rates with cumulative CO_2 production averaging 108 and 111 mg CO_2-C from *P. arundinacea* and mixed native root biomass, respectively (Table 13, Fig. 19b). Overall, irrespective of plant species, 23% of above-ground and 13% below-ground biomass C was released as CO_2 during the incubation study.

For the incubation conducted using soil collected from community B (Table 13, Fig. 20), the amount of CO_2 released from jars amended with *P. arundinacea* biomass was 1.7 (above-ground) to 1.3 fold (below-ground) higher than the amount produced from *S. cyperinus* (native sedge species). Thirty one percent of the C contained in the above-ground tissues of *P. arundinacea* was respired as CO_2, whereas, only 16% of the C contained in the above-ground biomass of *S. cyperinus* was released. These results indicate that the above-ground biomass of *P. arundinacea* was generally more decomposable than the above-ground tissues of *S. cyperinus*, producing 276 and 166 mg CO_2-C, respectively (Fig. 20a). Results for the below-ground biomass portion of the experiment exhibited the same pattern (Fig. 20b).

The lower CO_2 production with *S. cyperinus* biomass was consistent with the biochemical parameters for that species. All parameters indicated that *S. cyperinus* is more recalcitrant than the other species. Total CO_2 produced was inversely correlated with lignin to nitrogen ratio (r^2: 0.42, $P < 0.05$; Fig. 21). Other biochemical parameters (e.g. acid detergent fiber, lignin, cellulose, total phenolic content, C to N ratio, and plant nitrogen) were not significantly correlated with total CO_2 produced.

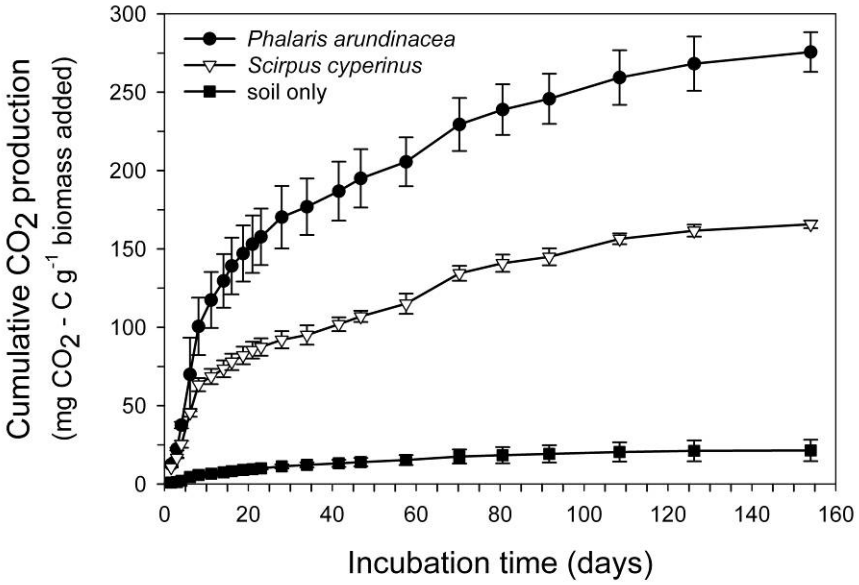


(a)

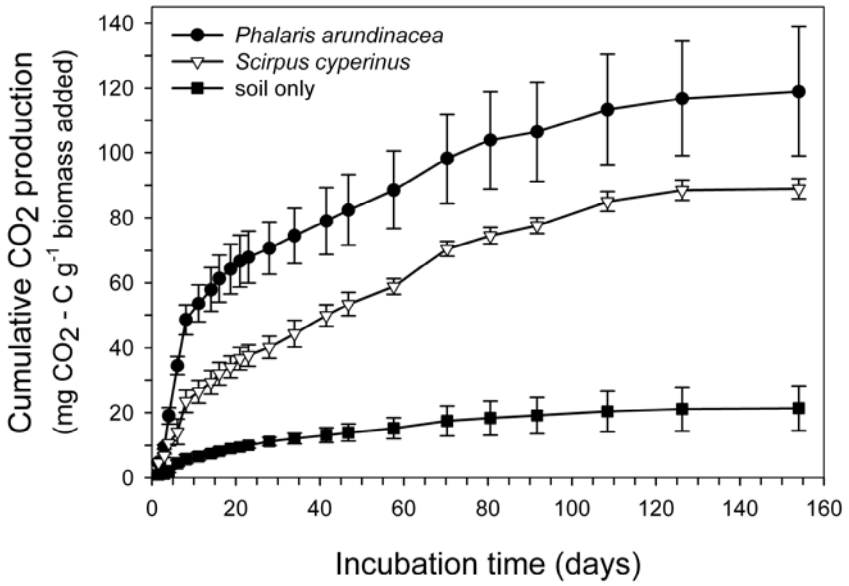


(b)

Figure 19. Decomposition experiment – Plant communities A and D. Cumulative CO_2 produced by biomass collected from the mixed native assemblage (Community A) and the *P. arundinacea* dominated plot (Community D). The biomass of these two species was incubated in soils collected from plant community A. (a) Above-ground biomass (shoots). (b) Below-ground biomass (roots). The whiskers represent the standard deviation from the mean ($n = 3$). †One sample jar was damaged half way through the experiment ($n = 2$).



(a)



(b)

Figure 20. Decomposition experiment – Plant communities B and C. Cumulative CO_2 produced by *S. cyperinus and P. arundinacea* collected from plant communities B and C, respectively. The biomass of these two species was incubated in soils collected from plant community B. (a) Above-ground biomass (shoots). (b) Below-ground biomass (roots). The whiskers represent the standard deviation from the mean (n = 3).

Table 13. Decomposition experiment – Summary results. Record of CO_2 produced in the decomposition experiment. Letters represent plant communities; community A was a mixed stand of 24 native species, community B was dominated by *S. cyperinus*, community C consisted of a monoculture of *P. arundinacea*, and community D was dominated by *P. arundinacea.* Biomass was incubated in soils collected from native plant communities (A and B). Tissue type refers to above and below-ground biomass.

Species	Soil	Tissue type	Plant community	cumulative residue C mineralized (mg CO_2 – C) – 154 days	residue carbon added mg organic carbon	carbon loss %
Phalaris arundinacea		above	D	257 ± 15[†]	880 ± 10	22
mixed native assemblage	A	above	A	270 ± 1[‡]	890 ± 50	24
soil only				61 ± 4		
Phalaris arundinacea		above	C	276 ± 13	824 ± 30	31
Scirpus cyperinus	B	above	B	166 ± 2	930 ± 4	16
soil only				21 ± 7		
Phalaris arundinacea		below	D	108 ± 12	404 ± 8	12
mixed native assemblage	A	below	A	111 ± 12	352 ± 4	14
soil only				61 ± 4		
Phalaris arundinacea		below	C	119 ± 20	406 ± 0	24
Scirpus cyperinus	B	below	B	89 ± 3	400 ± 0	17
soil only				21 ± 7		

[†] Plus or minus values represent the standard deviation from the mean (n = 3). [‡] For this particular set of data n = 2.

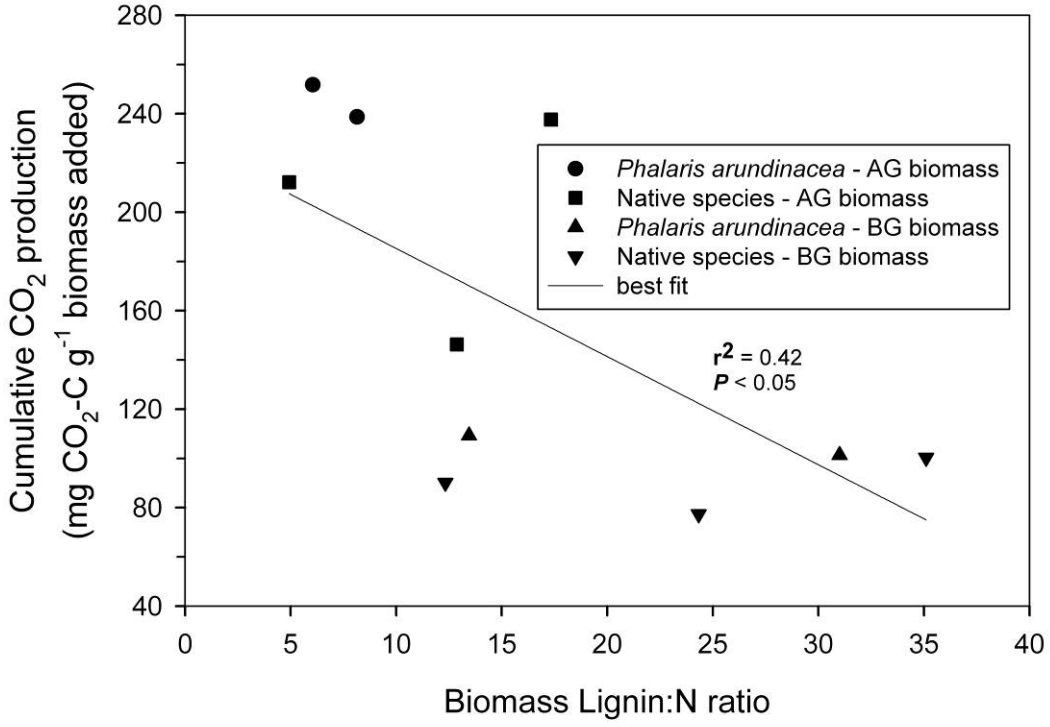


Figure 21. Correlation – Biomass lignin to nitrogen ratio vs. cumulative CO_2 production. The letters AG and BG represent above and below-ground biomass.

DISCUSSION

Factors Controlling Biomass Quality

Differences in plant biochemistry of *P. arundinacea* and the mixed native assemblage may be attributable to the different functional plant groups to which they belong. Plant community A consisted of 56% dicotyledons (dicots) and 44% monocotyledons (monocots). One of the physiological traits that distinguish dicots from monocots is the secondary growth that dicots experience into maturity. Dicots experience secondary growth of their xylem and phloem resulting in the formation of recalcitrant "woody" residues (Raven et al., 1999; Taiz and Zaiger, 2002). Xylem consists of lignified conduits used for fluid transport and plant support. Phloem consists of sieve elements, various kinds of parenchyma cells, fibers, and sclereids used for the transport of nutrients within the plant (Raven et al., 1999). This concentration of lignin late in the growth phase, explains why the mixed native assemblage of plant community A had such recalcitrant biomass. A look at the data for below ground biomass provides further evidence for this explanation of plant biochemistry. Roots from the mixed native assemblage, collected at the end of the growing season, contained twice as much lignin as roots collected in the middle of the growing season, whereas the lignin content of *P. arundinacea* roots did not differ between samplings during the growing season (Table 10).

Biochemical recalcitrance of species may also be related to their growth rate. De Deyn et al. (2008) reported that fast growing plants allocate most of their photosynthates to structures supporting photosynthesis, and therefore generate large quantities of biomass with low density, nutrient-rich and labile compounds. Shipley

(1989) investigated the relative growth rates of 68 herbaceous wetland angiosperms including *Juncus effusus* (*J. effusus*) and *S. cyperinus*, two species found at the study site. *J. effusus* was the eleventh fastest growing species of 68, whereas *S. cyperinus* grew more slowly than 67% of the other species tested. Biochemical data, collected during the current study, showed that *S. cyperinus*, the slower growing species was enriched in recalcitrant biomolecules (i.e. lignin and phenols).

Soil Organic Carbon Pools

1) Does hydroperiod have a dominant role in mediating SOC sequestration?

The primary motivation for this study was to determine whether *P. arundinacea* invasion had an impact on SOC pools in wetlands. One of the study hypotheses was that, this impact, if any, would be controlled by hydroperiod. The expectation was that SOC stocks would be greater in wetter areas. To verify this hypothesis, SOC stocks under *P. arundinacea* of community C (variably flooded with deep water) and community D (seasonally ponded) were compared using paired t-tests. There was no significant difference ($P > 0.05$) in the size of carbon pools within the two *P. arundinacea* invaded communities, 25.5 and 24.1 Mg C ha^{-1} for communities C and D, respectively. Correlating SOC pools using the hierarchy of wetness derived from the prevalence index (Tiner, 1999) showed that the lowest ranked community (A) in the hierarchy of wetness also had the smallest SOC stock, while the plot ranked as the wettest (B), did not have the largest SOC stores. These results, therefore, suggest a limited effect of hydroperiod on SOC stocks within wetlands.

2) Do diverse native plant assemblages result in larger soil organic carbon (SOC) stores in wetlands than monocultures of invasive P. arundinacea?

Carbon pools under the mixed native plant community A were compared to carbon pools under both *P. arundinacea* invaded plant communities C and D. Both *P. arundinacea* monocultures contained significantly ($P < 0.0001$) higher soil organic carbon pools (25.5 and 24.1 Mg C ha^{-1} for communities C and D, respectively) than the high diversity native plant assemblage (18.8 Mg C ha^{-1}). Therefore, although a high diversity of species has generally resulted in larger SOC pools in forest ecosystems (Jandl et al., 2007), it appears that with herbaceous wetlands the opposite may be true.

3) Does the biochemistry of different plant species have a dominant role in mediating carbon sequestration?

Carbon pools under plant community B dominated by *S. Cyperinus* were compared to pools under plant community C, one of the *P. arundinacea* invaded communities. Since both communities are established on the same soil type and experience similar hydroperiods, the effect of residue quality on SOC pool can be evaluated. There was no statistically significant difference in SOC pools between these two plots ($P > 0.05$).

Low residue quality, high biomass input, and low CO_2 production in the decomposition experiment suggested that the native species *S. cyperinus* is more recalcitrant and therefore SOC stocks under *S. cyperinus* should be greater than in areas invaded by *P. arundinacea*. The study results did not however, support the hypothesis that low residue quality (high lignin content, high phenolic content, and high C to N ratio) is conducive to SOC accumulation. In conjunction with the results

of the incubation study, biochemical parameters indicated that *P. arundinacea* biomass is less recalcitrant and should decompose fairly rapidly leading to lesser SOC storage. Yet, SOC pools under *P. arundinacea* were equal to or larger than pools in plots occupied by native species, whose biomass should be more recalcitrant and more conducive to formation of stable SOC pools given the results of the biochemical assays (Table 10). These results highlight the limitations of residue quality determined by laboratory assays as an approach to predict SOC sequestration in wetland ecosystems. At the field scale, there are probably additional factors regulating C dynamics which may not be fully simulated during laboratory tests. These factors may be more important than residue quality.

Decomposition generally involves depolymerization of lignin, as a way of accessing cellulose and hemicellulose sheltered by the bonding structure of lignin (Paul and Clark, 1996; Berg, 2000). Therefore, using values for biochemical molecules contained in plant biomass, obtained using conventional gravimetric techniques, appears to be ineffective at predicting field-scale decomposition and carbon sequestration. *In situ* field decomposition using litter bags may have been more effective at simulating factors controlling decomposition rates and organic matter accumulation at the field scale.

Hydrology and Microbial Diversity as Controls on Decomposition

After reviewing these observations, it seems plausible that something other than biomass quality or quantity controls carbon storage at the study site. It has been generally accepted that organic matter decomposition is restricted in wet environments (Stevenson, 1994). However, Mitsch and Gosselink (2000) reported

research results indicating that higher decay rates often occurred in wet environments when compared to dry environments; emphasizing that biomass decomposition is a complex process involving several factors with moisture, microbial community, and residue quality all having a role. Mitsch and Gosselink (2000) concluded that, in most cases, maximum biomass decomposition occurs in wet but not permanently flooded sites. Brinson et al. (1981) postulated that most rapid decomposition occurs in areas with fluctuating water tables, as long as periods of inundation do not generate complete anoxia. Evidence also exists suggesting that microbial diversity is reduced in soils that are saturated for lengthy periods (Zhou et al., 2002; Rinklebe and Langer, 2006). Rinklebe and Langer (2006) analyzed three floodplain soils of different flooding regimes for several parameters related to microbial diversity; phospholipid fatty acids, microbial carbon (C_{mic}), basal respiration, metabolic quotient, and C_{mic}/C_{org}. They found indirect relationships between flooding duration and microbial diversity. Those soils that were inundated the longest were shown to have the lowest microbial diversity based on all the parameters analyzed. Fog (1988) proposed that decomposer community may control decomposition more strongly than biomass quality. Several authors noted that diversity and composition of microbial communities significantly affect their ability to decompose plant matter (Wardle, 1998; Sinsabaugh et al., 2002; Rinklebe and Langer, 2006). Sinsabaugh et al. (2002) emphasized that no specific fungi or microbe has the enzymatic capability to decompose all components of plant residue by itself; microbes therefore must form mutually beneficial communities in soil ecosystems. It follows that reduced diversity prevents the microbial community from accessing all of the complex molecules that

may be available. Using these arguments, it is expected that decomposer communities are significantly more diverse in plant community A than in any other plant community at the site, given the hydrological characteristics of each plot. This would support greater decomposition rates among the mixed native species (community A) compared to other plant communities.

CONCLUSIONS

Past studies have reported mixed results concerning the impact of exotic plant invasion on terrestrial C storage. This is due in part to differences in soil types and the coexistence of various plant species in invaded ecosystems. *Phalaris arundinacea* is an herbaceous species that invades wetlands and floodplains throughout North America, including Beanblossom Bottoms - a wetland complex in south-central Indiana. Vegetation surveys showed monotypic stands of *Phalaris arundinacea* at different sites within Beanblossom Bottoms. It was expected that, due to its ability to grow prolifically and form monocultures, *Phalaris arundinacea* would alter soil carbon stocks and dynamics at invaded sites within the wetland complex. Past studies have shown that SOC stocks are generally greater in areas occupied by plant communities producing large amounts of biomass, having residue of low quality, or, a combination of these two factors. Oxygen limitation of decomposition processes in wet soils is another factor that has been linked to SOC accumulation. The present study was conducted with the objective of examining relationships between the residue quality of wetland plants and SOC stocks.

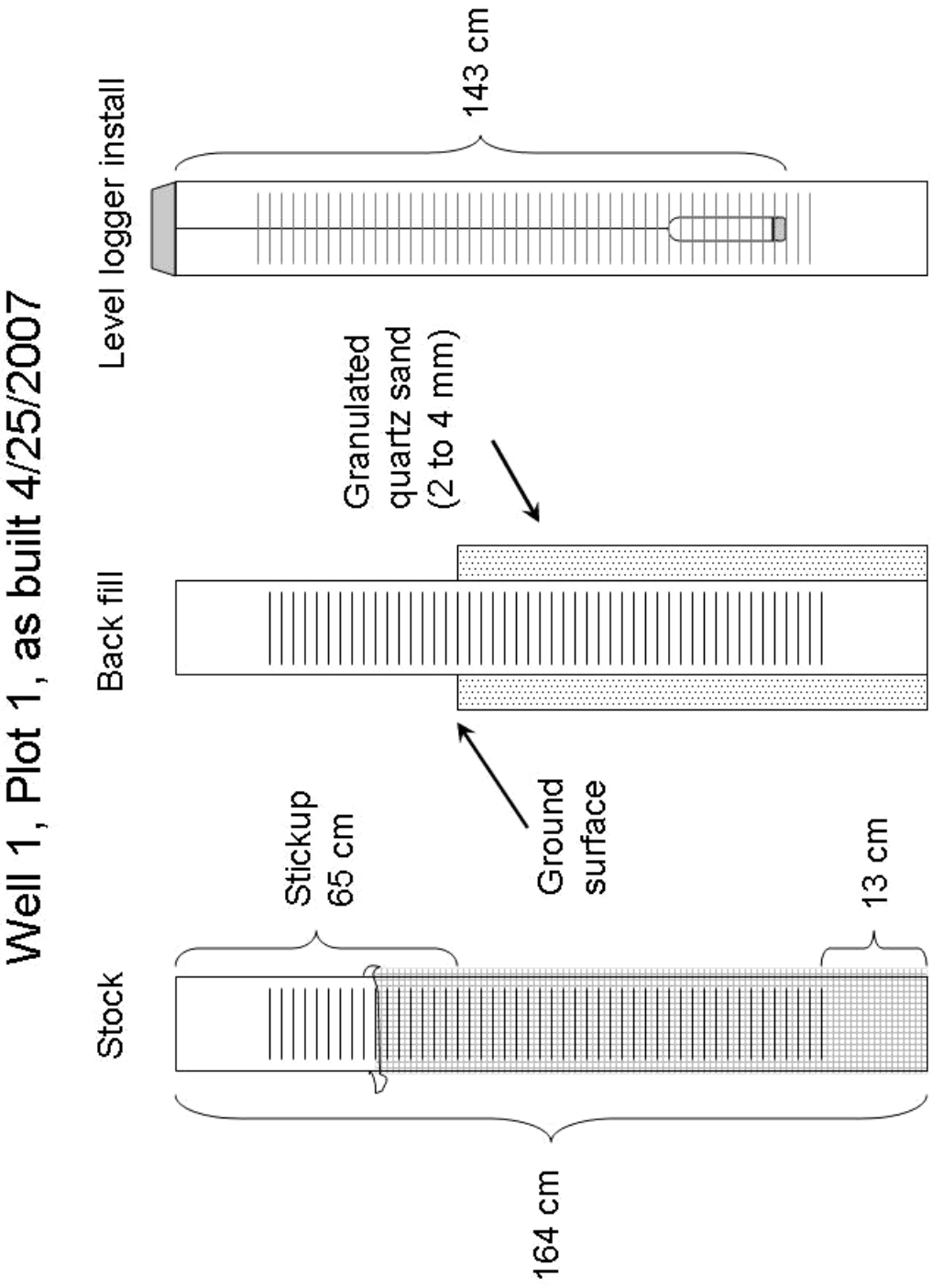
Results of the study showed that biomass production and residue quality were not good predictors of SOC pools at Beanblossom Bottoms. While *Scirpus cyperinus* (a native species) produced more biomass, its tissues decomposed less rapidly and contained greater concentrations of lignin and phenolics than *Phalaris arundinacea*, SOC stocks in areas invaded by *Phalaris arundinacea* were consistently (although not always significantly) greater than under *Scirpus cyperinus*. In addition, SOC stocks in a mixed native vegetation community (24 species) were 35% smaller than in

the monotypic stands of *Phalaris arundinacea.* It was also expected that by modulating the level of oxygen within the soil profile, hydroperiods could have a significant effect on SOC accumulation. Results of the study did not support this hypothesis.

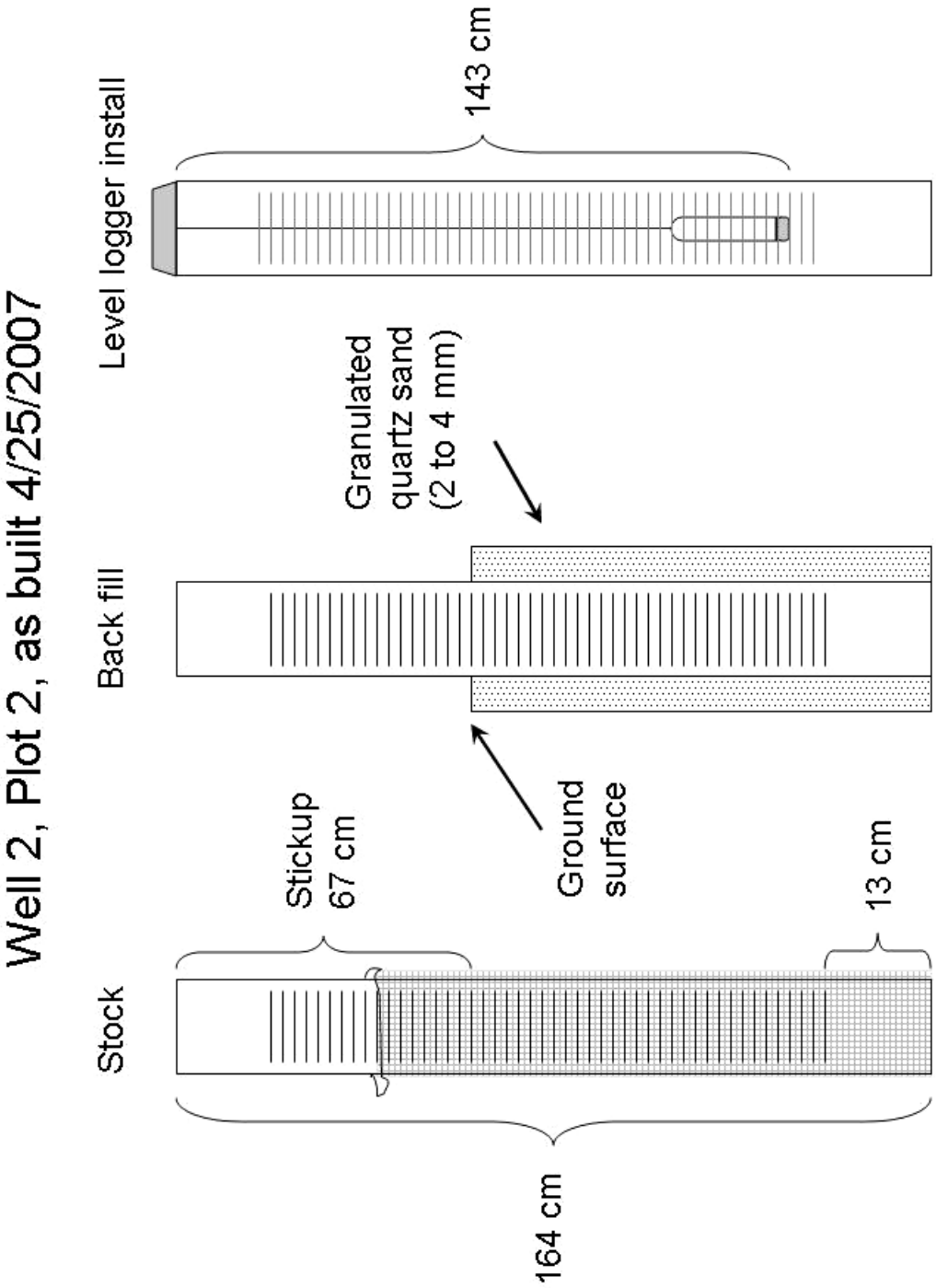
Overall, there was reasonable agreement among the laboratory data (residue biochemistry and incubation), but these laboratory results generally contradicted field measurements of SOC pools. It appears that laboratory experiments do not accurately account for all factors influencing SOC accumulation at the field scale. Instead of a "top-down" approach in which plant species and residue quality are considered as dominant controllers of SOC accumulation, a "bottom-up" approach where microbial community and soil structure are considered as dominant controllers of SOC accumulation may be a more appropriate model of ecosystem functioning at the study site. Future studies should consider microbial community, carbon chemistry, and soil structure, as additional drivers controlling the size and stability of SOC pools in this wetland complex.

LIMITATIONS

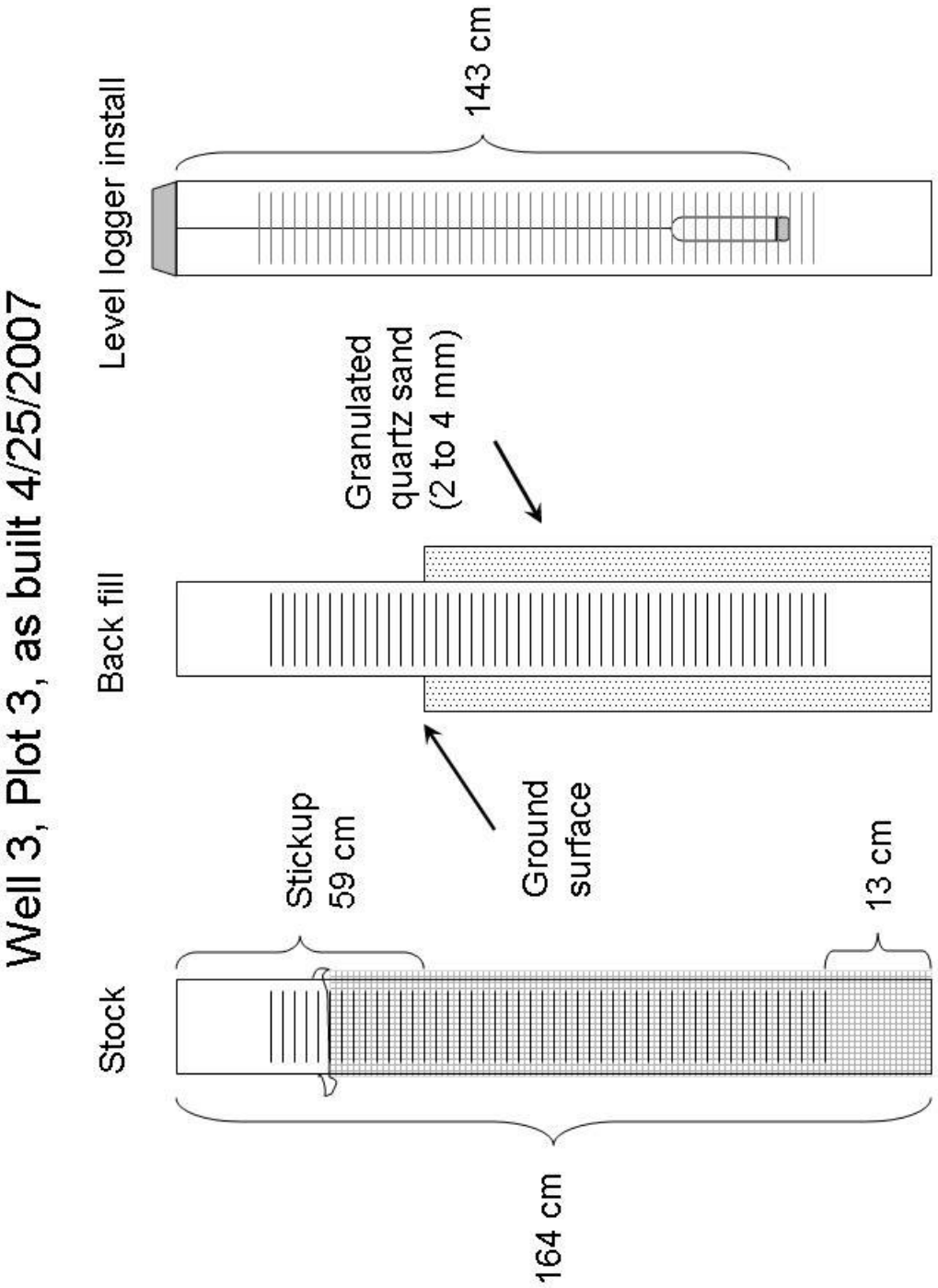
August, 2007 was the driest August recorded since 1938 with; precipitation totaling 1.07 cm in 2007 and 0.84 cm in 1938. During the last 100 years on record, average precipitation for the month of August is 9.55 cm (Indiana State Climate Office, 2008). Interestingly, spring 2008 was one of the wettest on record; total precipitation for May was 18.10 cm whereas average total precipitation for May is 11.73 cm. *Phalaris arundinacea* plots consisted of low, densely tangled mats no taller than 30-45 cm at both samplings in 2007. In contrast, *Phalaris arundinacea* stands were more than 2 meters in height, likely due to abundant rainfall, in spring 2008. In June 2008 *Scirpus cyperinus* had still not produced their large stalks, but consisted only of large bunches of grass no higher than 45 cm. These observations suggest that variation in the nature of hydroperiods from year to year may also affect the growth patterns of plant species at the site. De Deyn et al. (2008) postulate that plant growth rate governs biomass biochemistry and plants respond to environmental stressors by changing the ratio of recalcitrant to labile molecules in their tissues. These observations suggest that conducting the current study in other years might yield different results for biomass input, and possibly residue quality. It should also be noted that changes in total SOC stocks are generally slow; perhaps the 10-15 years since termination of agricultural activity at the site, is too short a period for plant communities to have a more noticeable affect on SOC pools.



Appendix A. Monitoring wells as built at Beanblossom Bottoms.



Appendix A (continued). Monitoring wells as built at Beanblossom Bottoms.



Appendix A (continued). Monitoring wells as built at Beanblossom Bottoms.

Appendix B. Soil physiochemical properties.

Soil physiochemical properties									
Plot #	Plant community	Quadrat	Plant species	depth (cm)	BD	pH	Sand	Silt	Clay
2	A	a	Mixed native	0-5	1.03	5.25	26.84	38.00	35.16
2	A	a	Mixed native	5-10	1.08	5.26	27.84	35.00	37.16
2	A	a	Mixed native	10-15	1.33	5.28	13.84	44.00	42.16
2	A	a	Mixed native	15-30	1.37	5.28	25.84	37.12	37.04
2	A	b	Mixed native	0-5	1.15	5.26	26.84	36.00	37.16
2	A	b	Mixed native	5-10	1.24	5.21	35.84	34.00	30.16
2	A	b	Mixed native	10-15	1.27	5.26	31.84	33.00	35.16
2	A	b	Mixed native	15-30	1.38	5.42	26.84	36.00	37.16
2	A	c	Mixed native	0-5	1.09	4.80	23.84	36.00	40.16
2	A	c	Mixed native	5-10	1.12	4.89	21.84	42.00	36.16
2	A	c	Mixed native	10-15	1.21	4.96	27.84	37.00	35.16
2	A	c	Mixed native	15-30	1.38	4.83	25.84	38.56	35.60
4	B	a	*Scirpus cyperinus*	0-5	1.23	4.80	25.84	32.00	42.16
4	B	a	*Scirpus cyperinus*	5-10	1.36	5.04	25.84	36.00	38.16
4	B	a	*Scirpus cyperinus*	10-15	1.35	5.68	26.84	29.00	44.16
4	B	a	*Scirpus cyperinus*	15-30	1.38	6.36	23.84	34.00	42.16
4	B	b	*Scirpus cyperinus*	0-5	1.15	4.60	19.84	34.00	46.16
4	B	b	*Scirpus cyperinus*	5-10	1.36	4.66	22.84	37.00	40.16
4	B	b	*Scirpus cyperinus*	10-15	1.32	5.54	41.84	27.00	31.16
4	B	b	*Scirpus cyperinus*	15-30	1.37	5.93	27.84	30.00	42.16
4	B	c	*Juncus effusus*	0-5	0.95	4.78	25.84	31.00	43.16
4	B	c	*Juncus effusus*	5-10	1.16	4.90	22.84	30.00	47.16
4	B	c	*Juncus effusus*	10-15	1.31	5.36	29.84	27.00	43.16
4	B	c	*Juncus effusus*	15-30	1.34	6.25	25.84	32.00	42.16

Appendix B continued. Soil physical properties.

Soil physiochemical properties, continued.									
Plot #	Plant community	Quadrat	Plant species	depth (cm)	BD	pH	Sand	Silt	Clay
3	C	a	*Phalaris arundinacea*	0-5	1.22	4.71	27.84	32.00	40.16
3	C	a	*Phalaris arundinacea*	5-10	1.38	5.17	23.84	35.00	41.16
3	C	a	*Phalaris arundinacea*	10-15	1.42	5.81	19.84	34.00	46.16
3	C	a	*Phalaris arundinacea*	15-30	1.46	6.38	31.48	29.64	38.88
3	C	b	*Phalaris arundinacea*	0-5	1.01	5.23	24.84	33.00	42.16
3	C	b	*Phalaris arundinacea*	5-10	1.37	5.50	24.84	31.00	44.16
3	C	b	*Phalaris arundinacea*	10-15	1.55	5.90	25.84	32.00	42.16
3	C	b	*Phalaris arundinacea*	15-30	1.44	6.26	29.84	28.00	42.16
3	C	c	*Phalaris arundinacea*	0-5	1.33	4.93	27.84	34.00	38.16
3	C	c	*Phalaris arundinacea*	5-10	1.37	5.00	39.84	34.00	26.16
3	C	c	*Phalaris arundinacea*	10-15	1.52	4.93	29.84	29.00	41.16
3	C	c	*Phalaris arundinacea*	15-30	1.62	5.86	29.48	33.64	36.88
1	D	a	*Phalaris arundinacea*	0-5	1.13	5.13	25.84	34.00	40.16
1	D	a	*Phalaris arundinacea*	5-10	1.29	5.26	29.84	37.00	33.16
1	D	a	*Phalaris arundinacea*	10-15	1.33	5.52	19.84	38.00	42.16
1	D	a	*Phalaris arundinacea*	15-30	1.35	5.79	25.48	35.64	38.88
1	D	b	*Phalaris arundinacea*	0-5	0.85	4.71	25.84	36.00	38.16
1	D	b	*Phalaris arundinacea*	5-10	1.17	5.03	27.84	34.00	38.16
1	D	b	*Phalaris arundinacea*	10-15	1.37	5.47	27.84	34.00	38.16
1	D	b	*Phalaris arundinacea*	15-30	1.47	5.38	27.84	35.00	37.16
1	D	c	*Phalaris arundinacea*	0-5	1.17	5.15	26.84	35.00	38.16
1	D	c	*Phalaris arundinacea*	5-10	1.30	5.34	8.84	35.00	56.16
1	D	c	*Phalaris arundinacea*	10-15	1.36	5.65	33.84	38.00	28.16
1	D	c	*Phalaris arundinacea*	15-30	1.37	5.67	25.84	34.00	40.16

Appendix C. Below-ground biomass.

Below-ground biomass collected during the growing season						
Plot #	**Plant community**	**Quadrat**	**Plant species**	**Depth interval**	**Middle-of-season**	**End-of-season**
				(cm)	mass, g	mass, g
2	A	a	Mixed natives	0-5	11.801	5.070
2	A	a	Mixed natives	5-10	0.927	0.413
2	A	a	Mixed natives	10-15	0.134	0.172
2	A	a	Mixed natives	15-30	0.142	0.065
2	A	b	Mixed natives	0-5	9.563	12.080
2	A	b	Mixed natives	5-10	2.491	0.770
2	A	b	Mixed natives	10-15	0.508	0.140
2	A	b	Mixed natives	15-30	0.556	0.110
2	A	c	Mixed natives	0-5	9.291	3.670
2	A	c	Mixed natives	5-10	1.540	0.366
2	A	c	Mixed natives	10-15	0.498	0.122
2	A	c	Mixed natives	15-30	0.467	0.026
4	B	a	*Scirpus cyperinus*	0-5	2.818	26.250
4	B	a	*Scirpus cyperinus*	5-10	1.213	2.240
4	B	a	*Scirpus cyperinus*	10-15	0.430	0.151
4	B	a	*Scirpus cyperinus*	15-30	0.497	0.493
4	B	b	*Scirpus cyperinus*	0-5	17.009	15.920
4	B	b	*Scirpus cyperinus*	5-10	2.394	1.291
4	B	b	*Scirpus cyperinus*	10-15	0.341	1.022
4	B	b	*Scirpus cyperinus*	15-30	0.537	1.186
4	B	c	*Juncus effusus*	0-5	18.647	9.057
4	B	c	*Juncus effusus*	5-10	0.903	0.657
4	B	c	*Juncus effusus*	10-15	0.924	0.441
4	B	c	*Juncus effusus*	15-30	0.395	0.187
3	C	a	*Phalaris arundinacea*	0-5	11.898	5.380
3	C	a	*Phalaris arundinacea*	5-10	1.230	0.970
3	C	a	*Phalaris arundinacea*	10-15	0.247	0.414
3	C	a	*Phalaris arundinacea*	15-30	0.317	0.271
3	C	b	*Phalaris arundinacea*	0-5	19.222	4.550
3	C	b	*Phalaris arundinacea*	5-10	1.188	0.244
3	C	b	*Phalaris arundinacea*	10-15	0.173	0.142
3	C	b	*Phalaris arundinacea*	15-30	0.364	0.214
3	C	c	*Phalaris arundinacea*	0-5	13.082	6.230
3	C	c	*Phalaris arundinacea*	5-10	1.070	0.478
3	C	c	*Phalaris arundinacea*	10-15	0.454	0.177
3	C	c	*Phalaris arundinacea*	15-30	1.533	0.273
1	D	a	*Phalaris arundinacea*	0-5	10.684	14.810
1	D	a	*Phalaris arundinacea*	5-10	2.487	1.872
1	D	a	*Phalaris arundinacea*	10-15	0.961	0.204
1	D	a	*Phalaris arundinacea*	15-30	1.055	0.259
1	D	b	*Phalaris arundinacea*	0-5	8.664	4.620
1	D	b	*Phalaris arundinacea*	5-10	5.124	4.240
1	D	b	*Phalaris arundinacea*	10-15	1.023	0.620
1	D	b	*Phalaris arundinacea*	15-30	1.573	0.460
1	D	c	*Phalaris arundinacea*	0-5	12.041	9.710
1	D	c	*Phalaris arundinacea*	5-10	4.172	3.230
1	D	c	*Phalaris arundinacea*	10-15	1.031	0.697
1	D	c	*Phalaris arundinacea*	15-30	0.840	0.802

Appendix D. Soil organic carbon and nitrogen.

Soil organic carbon and nitrogen							
Plot #	**Plant community**	**Plant species**	**Field replicates**	**Quadrat**	**Depth (cm)**	**N g kg^{-1}**	**C g kg^{-1}**
2	A	Mixed natives	1†	a	0-5	1.350	13.155
2	A	Mixed natives	1	a	5-10	1.150	8.873
2	A	Mixed natives	1	a	10-15	1.016	6.382
2	A	Mixed natives	1	a	15-30	0.885	4.835
2	A	Mixed natives	2	a	0-5	1.106	8.633
2	A	Mixed natives	2	a	5-10	0.984	6.576
2	A	Mixed natives	2	a	10-15	0.923	5.446
2	A	Mixed natives	2	a	15-30	0.893	4.631
2	A	Mixed natives	1	b	0-5	1.076	11.383
2	A	Mixed natives	1	b	5-10	0.708	6.387
2	A	Mixed natives	1	b	10-15	0.573	5.496
2	A	Mixed natives	1	b	15-30	0.562	5.020
2	A	Mixed natives	2	b	0-5	0.677	7.681
2	A	Mixed natives	2	b	5-10	0.688	7.601
2	A	Mixed natives	2	b	10-15	0.511	5.233
2	A	Mixed natives	2	b	15-30	0.511	5.199
2	A	Mixed natives	1	c	0-5	0.576	10.245
2	A	Mixed natives	1	c	5-10	0.309	6.207
2	A	Mixed natives	1	c	10-15	0.213	4.867
2	A	Mixed natives	1	c	15-30	0.074	3.573
2	A	Mixed natives	2	c	0-5	0.311	6.845
2	A	Mixed natives	2	c	5-10	0.176	5.504
2	A	Mixed natives	2	c	10-15	0.216	4.755
2	A	Mixed natives	2	c	15-30	0.062	3.469
4	B	*Scirpus cyperinus*	1	a	0-5	1.220	10.971
4	B	*Scirpus cyperinus*	1	a	5-10	0.868	5.158
4	B	*Scirpus cyperinus*	1	a	10-15	0.671	4.364
4	B	*Scirpus cyperinus*	1	a	15-30	0.368	2.338
4	B	*Scirpus cyperinus*	2	a	0-5	1.515	14.986
4	B	*Scirpus cyperinus*	2	a	5-10	1.027	7.667
4	B	*Scirpus cyperinus*	2	a	10-15	1.012	7.660
4	B	*Scirpus cyperinus*	2	a	15-30	0.887	2.667
4	B	*Scirpus cyperinus*	1	b	0-5	1.527	15.255
4	B	*Scirpus cyperinus*	1	b	5-10	0.916	6.579
4	B	*Scirpus cyperinus*	1	b	10-15	0.888	5.597
4	B	*Scirpus cyperinus*	1	b	15-30	0.837	4.463
4	B	*Scirpus cyperinus*	2	b	0-5	1.418	16.128
4	B	*Scirpus cyperinus*	2	b	5-10	0.722	7.319
4	B	*Scirpus cyperinus*	2	b	10-15	0.602	5.991
4	B	*Scirpus cyperinus*	2	b	15-30	0.505	4.995
4	B	*Juncus effusus*	1	c	0-5	1.335	10.138
4	B	*Juncus effusus*	1	c	5-10	1.213	8.492
4	B	*Juncus effusus*	1	c	10-15	1.051	6.774
4	B	*Juncus effusus*	1	c	15-30	0.868	3.929
4	B	*Juncus effusus*	2	c	0-5	1.669	14.723
4	B	*Juncus effusus*	2	c	5-10	1.261	9.163
4	B	*Juncus effusus*	2	c	10-15	1.174	8.194
4	B	*Juncus effusus*	2	c	15-30	0.940	5.310

Appendix D continued. Soil organic carbon and nitrogen.

Soil organic carbon and nitrogen, continued.							
Plot #	**Plant Community**	**Plant species**	**Field replicates**	**Quadrat**	**Depth (cm)**	**N g kg^{-1}**	**C g kg^{-1}**
3	C	*Phalaris arundinacea*	1	a	0-5	1.617	15.695
3	C	*Phalaris arundinacea*	1	a	5-10	1.183	9.419
3	C	*Phalaris arundinacea*	1	a	10-15	1.026	7.524
3	C	*Phalaris arundinacea*	1	a	15-30	0.867	4.967
3	C	*Phalaris arundinacea*	2	a	0-5	1.333	11.704
3	C	*Phalaris arundinacea*	2	a	5-10	1.126	8.340
3	C	*Phalaris arundinacea*	2	a	10-15	1.045	7.375
3	C	*Phalaris arundinacea*	2	a	15-30	0.888	5.030
3	C	*Phalaris arundinacea*	1	b	0-5	1.642	16.781
3	C	*Phalaris arundinacea*	1	b	5-10	0.953	8.316
3	C	*Phalaris arundinacea*	1	b	10-15	0.814	7.283
3	C	*Phalaris arundinacea*	1	b	15-30	0.433	3.522
3	C	*Phalaris arundinacea*	2	b	0-5	1.249	13.005
3	C	*Phalaris arundinacea*	2	b	5-10	0.811	8.177
3	C	*Phalaris arundinacea*	2	b	10-15	0.705	7.112
3	C	*Phalaris arundinacea*	2	b	15-30	0.528	5.370
3	C	*Phalaris arundinacea*	1	c	0-5	1.491	11.121
3	C	*Phalaris arundinacea*	1	c	5-10	1.225	7.723
3	C	*Phalaris arundinacea*	1	c	10-15	0.948	4.814
3	C	*Phalaris arundinacea*	1	c	15-30	0.880	3.523
3	C	*Phalaris arundinacea*	2	c	0-5	1.616	11.999
3	C	*Phalaris arundinacea*	2	c	5-10	1.428	9.549
3	C	*Phalaris arundinacea*	2	c	10-15	1.319	7.923
3	C	*Phalaris arundinacea*	2	c	15-30	1.067	5.709
1	D	*Phalaris arundinacea*	1	a	0-5	2.150	22.148
1	D	*Phalaris arundinacea*	1	a	5-10	1.053	10.492
1	D	*Phalaris arundinacea*	1	a	10-15	0.824	6.807
1	D	*Phalaris arundinacea*	1	a	15-30	0.613	4.543
1	D	*Phalaris arundinacea*	2	a	0-5	1.683	16.628
1	D	*Phalaris arundinacea*	2	a	5-10	0.976	7.176
1	D	*Phalaris arundinacea*	2	a	10-15	0.626	5.266
1	D	*Phalaris arundinacea*	2	a	15-30	0.521	4.578
1	D	*Phalaris arundinacea*	1	b	0-5	1.485	12.233
1	D	*Phalaris arundinacea*	1	b	5-10	0.983	5.769
1	D	*Phalaris arundinacea*	1	b	10-15	0.911	4.687
1	D	*Phalaris arundinacea*	1	b	15-30	0.951	5.026
1	D	*Phalaris arundinacea*	2	b	0-5	2.044	18.785
1	D	*Phalaris arundinacea*	2	b	5-10	1.384	10.621
1	D	*Phalaris arundinacea*	2	b	10-15	1.047	6.617
1	D	*Phalaris arundinacea*	2	b	15-30	0.937	4.720
1	D	*Phalaris arundinacea*	1	c	0-5	2.119	20.688
1	D	*Phalaris arundinacea*	1	c	5-10	0.848	7.206
1	D	*Phalaris arundinacea*	1	c	10-15	0.742	5.713
1	D	*Phalaris arundinacea*	1	c	15-30	0.443	3.458
1	D	*Phalaris arundinacea*	2	c	0-5	1.463	13.031
1	D	*Phalaris arundinacea*	2	c	5-10	1.026	7.334
1	D	*Phalaris arundinacea*	2	c	10-15	0.899	5.514
1	D	*Phalaris arundinacea*	2	c	15-30	0.345	2.389

Appendix E. Plant biochemistry. Above-ground biomass collected during the middle of the growing season.

Plant biochemistry, above-ground biomass collected during the middle of the growing season											
Plant community	Plant species	Quadrat	Replicate	Acid det. fiber	Cellulose	Lignin	Phenolics	Carbon	Nitrogen	C:N	Lignin:N
				g kg^{-1}							
A	Mixed natives	a	1	56.486	239.567	107.143	41.599	364.360	10.153	35.887	12.176
A	Mixed natives	a	2	55.818	238.865	98.147	38.724	363.792	9.929	36.639	11.731
A	Mixed natives	b	1	51.489	201.296	138.010	30.486	247.187	7.854	31.474	20.927
A	Mixed natives	b	2	51.686	225.794	117.872	32.381	248.328	7.928	31.323	20.457
A	Mixed natives	c	1	40.508	130.026	106.351	33.614	290.059	9.099	31.878	9.504
A	Mixed natives	c	2	41.117	105.181	104.792	34.571	293.678	9.262	31.708	8.250
B	*Scirpus cyperinus*	a	1	54.815	255.814	123.623	40.650	413.258	12.157	33.993	6.152
B	*Scirpus cyperinus*	a	2	53.217	276.825	116.474	43.468	414.852	12.053	34.419	6.063
B	*Scirpus cyperinus*	b	1	50.297	242.670	164.352	37.269	399.369	14.473	27.593	4.478
B	*Scirpus cyperinus*	b	2	49.960	251.345	162.183	36.390	394.187	14.243	27.676	4.591
B	*Juncus effusus*	c	1	62.085	165.487	86.478	13.295	392.873	17.700	22.196	4.467
B	*Juncus effusus*	c	2	62.685	165.026	76.408	15.543	396.514	17.517	22.636	4.428
C	*Phalaris arundinacea*	a	1	51.317	170.441	90.584	6.400	277.071	14.887	18.612	6.085
C	*Phalaris arundinacea*	a	2	52.669	170.603	83.876	6.146	286.168	15.315	18.686	5.477
C	*Phalaris arundinacea*	b	1	58.304	252.322	75.077	13.020	376.523	16.592	22.694	4.525
C	*Phalaris arundinacea*	b	2	58.534	246.789	74.348	12.043	378.140	16.665	22.690	4.461
C	*Phalaris arundinacea*	c	1	58.013	219.055	79.805	10.125	375.407	16.416	22.868	4.861
C	*Phalaris arundinacea*	c	2	58.674	220.692	75.924	9.299	375.333	16.290	23.040	4.661
D	*Phalaris arundinacea*	a	1	55.916	195.818	74.789	8.649	260.918	13.806	18.899	7.761
D	*Phalaris arundinacea*	a	2	56.353	194.638	73.081	9.318	258.396	13.686	18.880	7.171
D	*Phalaris arundinacea*	b	1	58.611	189.564	64.819	17.447	276.912	13.940	19.864	9.900
D	*Phalaris arundinacea*	b	2	56.829	204.147	65.391	16.755	275.646	13.700	20.120	8.604
D	*Phalaris arundinacea*	c	1	48.012	156.273	79.065	8.875	302.077	15.621	19.338	6.808
D	*Phalaris arundinacea*	c	2	48.900	143.143	77.569	8.782	297.241	15.506	19.170	6.758

Appendix E continued. Plant biochemistry. Above-ground biomass collected at the end of the growing season.

Plant biochemistry, above-ground biomass collected at the end of the growing season											
Plant community	Plant species	Quadrat	Replicate	Acid det. fiber	Cellulose	Lignin	Phenolics	Carbon	Nitrogen	C:N	Lignin:N
				g kg^{-1}							
A	Mixed natives	a	1	48.363	299.315	153.465	28.663	241.009	6.415	37.570	23.577
A	Mixed natives	a	2	47.845	286.279	178.727	29.080				
A	Mixed natives	b	1	47.939	273.664	159.160	17.746	201.284	6.002	33.536	27.550
A	Mixed natives	b	2	47.430	289.872	149.282	19.606				
A	Mixed natives	c	1	44.144	204.766	180.533	24.174	171.249	5.462	31.353	13.510
A	Mixed natives	c	2	46.978	192.700	164.443	26.357				
B	*Scirpus cyperinus*	a	1	49.961	311.820	151.244	25.498	198.594	8.382	23.693	7.565
B	*Scirpus cyperinus*	a	2	51.052	293.453	165.627	23.230				
B	*Scirpus cyperinus*	b	1	49.646	294.882	165.354	19.903	222.548	9.670	23.014	6.071
B	*Scirpus cyperinus*	b	2	49.717	287.439	176.914	19.685				
B	*Juncus effusus*	c	1	62.425	283.606	73.793	22.216	168.595	6.853	24.602	11.597
B	*Juncus effusus*	c	2	87.539	284.766	69.141	23.556				
C	*Phalaris arundinacea*	a	1	59.028	164.352	97.608	12.211	221.235	13.744	16.097	7.102
C	*Phalaris arundinacea*	a	2	59.207	164.900	102.473	11.999				
C	*Phalaris arundinacea*	b	1	64.356	198.897	61.442	19.591	256.013	14.670	17.451	4.188
C	*Phalaris arundinacea*	b	2	65.621	197.697	50.814	21.875				
C	*Phalaris arundinacea*	c	1	60.183	176.166	80.909	17.282	224.897	14.950	15.043	5.412
C	*Phalaris arundinacea*	c	2	60.979	171.011	85.308	16.624				
D	*Phalaris arundinacea*	a	1	31.207	78.786	63.413	6.117	85.248	4.526	18.835	33.908
D	*Phalaris arundinacea*	a	2	31.128	94.859	58.191	5.846				
D	*Phalaris arundinacea*	b	1	28.281	83.269	58.711	6.512	118.057	5.952	19.835	26.741
D	*Phalaris arundinacea*	b	2	29.810	76.010	53.840	6.915				
D	*Phalaris arundinacea*	c	1	57.176	197.145	79.475	11.214	222.077	11.088	20.029	16.282
D	*Phalaris arundinacea*	c	2	56.823	197.764	81.342	12.433				

Appendix E continued. Plant biochemistry. Below-ground biomass collected during the middle of the growing season.

Plant biochemistry, below-ground biomass collected during the middle of the growing season											
Plant community	Plant species	Quadrat	Replicate	Acid det. fiber	Cellulose	Lignin	Phenolics	Carbon	Nitrogen	C:N	Lignin:N
				g kg^{-1}							
A	Mixed natives	a	1	13.112	44.084	53.881	9.478	70.239	2.853	24.619	56.228
A	Mixed natives	a	2	14.831	42.093	52.321	9.754	69.694	3.276	21.272	45.433
A	Mixed natives	b	1	31.111	105.461	122.034	15.907	212.596	6.091	34.903	31.867
A	Mixed natives	b	2	31.274	114.152	109.461	17.025	212.336	6.151	34.521	28.574
A	Mixed natives	c	1	17.572	47.923	79.473	11.672	108.985	4.655	23.413	19.867
A	Mixed natives	c	2	18.984	61.387	79.955	11.873	111.387	4.358	25.558	21.350
B	*Scirpus cyperinus*	a	1	41.361	184.383	160.417	14.182	326.617	8.551	38.196	10.730
B	*Scirpus cyperinus*	a	2	42.328	164.504	148.855	14.094	304.685	8.458	36.022	11.814
B	*Scirpus cyperinus*	b	1	32.466	159.648	194.104	26.341	256.366	9.484	27.032	6.791
B	*Scirpus cyperinus*	b	2	32.580	171.083	175.760	26.637	260.948	9.712	26.870	6.768
B	*Juncus effusus*	c	1	31.053	57.519	92.481	9.432	144.785	7.785	18.597	15.053
B	*Juncus effusus*	c	2	31.257	63.806	93.050	9.797	144.811	7.846	18.457	14.451
C	*Phalaris arundinacea*	a	1	32.096	87.988	90.666	2.732	177.041	9.740	18.176	9.308
C	*Phalaris arundinacea*	a	2	31.903	96.132	85.408	2.617	173.588	9.387	18.492	9.098
C	*Phalaris arundinacea*	b	1	29.806	58.660	95.521	3.159	169.487	10.028	16.901	9.525
C	*Phalaris arundinacea*	b	2	28.424	76.831	106.290	3.258	170.194	9.706	17.536	10.951
C	*Phalaris arundinacea*	c	1	38.252	121.831	118.804	4.197	239.610	11.884	20.162	9.997
C	*Phalaris arundinacea*	c	2	38.186	122.434	117.954	4.180	244.456	12.020	20.337	9.813
D	*Phalaris arundinacea*	a	1	45.802	157.504	91.753	2.441	98.879	4.936	20.032	10.916
D	*Phalaris arundinacea*	a	2	46.934	160.863	99.924	2.620	120.750	5.293	22.814	9.885
D	*Phalaris arundinacea*	b	1	30.428	72.117	64.404	2.142	116.926	4.072	28.717	29.972
D	*Phalaris arundinacea*	b	2	32.371	75.988	65.729	2.507	127.698	4.306	29.653	25.418
D	*Phalaris arundinacea*	c	1	46.877	166.924	117.194	3.343	120.283	4.890	24.599	16.253
D	*Phalaris arundinacea*	c	2	48.478	166.266	113.381	3.694	125.686	5.023	25.021	15.917

Appendix E continued. Plant biochemistry. Below-ground biomass collected at the end of the growing season.

Plant biochemistry, below-ground biomass collected at the end of the growing season											
Plant community	Plant species	Quadrat	Replicate	Acid det. Fiber	Cellulose	Lignin	Phenolics	Carbon	Nitrogen	C:N	Lignin:N
				g kg^{-1}							
A	Mixed natives	a	1	51.558	206.144	198.575	23.155	196.846	5.934	33.173	31.429
A	Mixed natives	a	2	50.724	223.782	189.557	22.996	197.302	5.963	33.088	32.383
A	Mixed natives	b	1	56.558	194.466	175.512	54.810	175.862	6.706	26.225	28.917
A	Mixed natives	b	2	55.079	209.449	181.102	55.494	182.317	6.794	26.835	28.370
A	Mixed natives	c	1	51.590	211.229	166.078	25.122	142.627	5.092	28.010	24.578
A	Mixed natives	c	2	51.717	215.949	170.944	30.177	149.005	5.067	29.407	20.296
B	*Scirpus cyperinus*	a	1	42.971	206.070	186.502	43.223	201.008	8.450	23.788	10.904
B	*Scirpus cyperinus*	a	2	43.607	195.726	193.101	44.315	207.430	8.589	24.151	11.656
B	*Scirpus cyperinus*	b	1	53.022	206.491	193.915	37.554	235.328	9.904	23.761	12.657
B	*Scirpus cyperinus*	b	2	48.601	251.872	192.747	37.210	225.953	9.672	23.362	11.497
B	*Juncus effusus*	c	1	52.442	159.871	125.151	10.380	172.695	7.041	24.527	17.283
B	*Juncus effusus*	c	2	36.012	105.418	102.838	10.431	159.021	6.808	23.358	14.437
C	*Phalaris arundinacea*	a	1	53.576	191.969	132.696	11.024	181.117	8.248	21.959	16.088
C	*Phalaris arundinacea*	a	2	53.407	194.171	132.854	11.458	180.965	8.294	21.819	16.018
C	*Phalaris arundinacea*	b	1	57.357	186.784	103.084	5.497	158.625	7.604	20.861	13.557
C	*Phalaris arundinacea*	b	2	48.844	191.781	107.877	5.114	172.402	8.251	20.895	13.074
C	*Phalaris arundinacea*	c	1	52.355	216.248	120.487	4.656	176.004	7.219	24.381	16.690
C	*Phalaris arundinacea*	c	2	53.831	203.652	128.622	4.964	176.227	7.262	24.267	17.712
D	*Phalaris arundinacea*	a	1	45.552	146.148	92.137	2.756	92.802	3.954	23.470	50.221
D	*Phalaris arundinacea*	a	2	47.730	143.578	100.116	2.942	98.781	4.017	24.591	47.189
D	*Phalaris arundinacea*	b	1	60.868	192.447	125.352	4.177	204.823	6.873	29.801	25.536
D	*Phalaris arundinacea*	b	2	60.575	208.787	111.198	4.703	197.464	6.907	28.589	26.220
D	*Phalaris arundinacea*	c	1	55.820	204.460	121.693	5.123	169.186	6.400	26.435	25.950
D	*Phalaris arundinacea*	c	2	58.138	189.415	98.289	5.466	159.131	6.251	25.457	27.347

Appendix F. Cumulative CO_2 produced during the decomposition experiment. Above-ground biomass collected during the middle of the growing season.

Cumulative CO_2 Produced (mg CO_2 - C)											
Above-ground biomass											
Incubation	Mixed native plants		*Scirpus cyperinus* dominated plot			*Phalaris arundinacea* monoculture			*Phalaris arundinacea* dominated plot		
	Plant community A		Plant community B			Plant community C			Plant community D		
time (days)	Jar 1	Jar 2	Jar 1	Jar 2	Jar 3	Jar 1	Jar 2	Jar 3	Jar 1	Jar 2	Jar 3
2	14.211	13.399	10.473	10.730	10.693	12.672	12.899	11.575	12.191	10.829	12.540
3	22.456	22.852	16.754	16.371	16.735	22.858	22.695	21.338	20.600	18.011	20.155
4	34.691	39.409	22.967	27.373	25.799	37.326	35.628	39.783	36.257	34.633	34.561
6	60.422	65.475	43.136	48.098	44.968	85.951	80.788	43.016	66.982	63.753	66.410
8	70.728	78.672	59.201	67.628	63.353	112.466	109.665	79.453	75.831	75.173	75.997
11	77.692	86.781	63.489	73.291	68.881	129.381	125.983	96.836	82.999	84.068	84.381
14	84.028	94.287	67.860	78.556	74.029	142.541	136.101	110.166	89.795	91.504	91.176
16	89.312	99.877	72.419	82.788	78.598	152.596	146.158	118.579	95.972	96.918	97.026
19	94.485	105.390	76.190	87.376	82.437	160.693	153.606	126.771	101.197	102.819	102.999
21	98.929	109.609	79.965	90.675	85.439	166.311	160.521	132.100	106.488	107.315	107.679
23	102.417	113.334	81.853	92.963	87.332	171.087	164.807	137.171	109.928	111.398	111.435
28	112.779	123.464	87.349	98.029	90.604	185.386	177.638	147.687	121.619	122.462	123.120
34	122.131	131.995	91.278	102.221	91.733	189.989	184.271	156.358	134.978	134.434	133.972
42	134.175	142.078	99.707	107.019	99.065	200.644	194.386	165.415	157.233	151.185	151.216
47	144.055	151.055	104.036	110.922	105.733	208.459	202.828	173.736	161.950	159.694	159.624
58	164.193	173.199	111.185	122.446	111.418	218.344	210.158	188.140	183.462	179.622	177.060
70	198.095	204.977	130.878	139.825	132.498	242.450	235.427	210.259	206.928	199.600	189.217
81	218.953	224.178	138.187	147.151	137.196	253.202	241.968	221.369	223.497	214.614	205.781
92	230.818	237.273	143.153	151.005	140.613	260.455	248.087	228.722	232.803	223.854	216.702
108	256.303	268.797	155.160	160.261	153.721	277.460	257.830	242.717	253.986	245.133	239.258
126	269.730	269.097	161.525	165.438	157.801	286.443	266.049	252.029	266.600	257.452	239.813
154	270.940	269.929	163.186	165.890	167.941	287.379	277.203	262.178	269.361	261.172	241.107

Appendix F continued. Cumulative CO_2 produced during the decomposition experiment. Below-ground biomass collected during the middle of the growing season.

Cumulative CO_2 Produced (mg CO_2 - C)												
Below-ground biomass												
Incubation	Mixed Natives			*Scirpus cyperinus* dominated plot			*Phalaris arundinacea* monoculture			*Phalaris arundinacea* dominated plot		
	Plant Community A			Plant Community B			Plant Community C			Plant community D		
time (days)	Jar 1	Jar 2	Jar 3	Jar 1	Jar 2	Jar 3	Jar 1	Jar 2	Jar 3	Jar 1	Jar 2	Jar 3
2	5.108	6.710	4.966	4.478	4.520	4.948	4.215	4.659	5.147	6.513	6.476	7.981
3	7.677	10.312	7.646	6.317	6.451	7.358	8.779	10.206	9.544	9.877	10.094	11.738
4	11.885	15.601	12.517	9.992	10.521	11.451	18.685	21.759	16.752	16.293	17.854	17.956
6	21.286	26.689	24.284	18.552	11.190	12.866	34.238	37.494	31.900	30.011	31.465	33.688
8	27.013	32.768	29.802	27.365	20.933	22.149	48.173	53.430	44.200	35.548	36.685	39.415
11	30.176	36.582	33.547	30.403	23.969	25.014	54.017	59.112	47.680	39.606	40.465	43.731
14	33.623	40.218	37.048	33.437	26.452	28.070	59.039	63.936	50.634	42.731	43.814	47.182
16	36.194	43.296	40.233	36.053	29.296	30.684	62.853	67.650	53.401	45.587	46.401	50.120
19	38.939	46.154	43.301	37.815	31.216	33.356	65.962	70.873	55.780	48.579	48.699	53.002
21	40.975	48.426	45.494	40.541	33.866	35.622	68.306	73.615	57.943	50.967	50.897	55.285
23	42.662	50.858	47.798	41.382	35.106	36.610	69.703	74.751	59.210	52.901	52.774	56.725
28	48.457	57.099	53.302	44.019	37.850	38.675	72.947	77.273	61.710	58.793	57.879	61.945
34	52.563	61.814	58.057	48.841	41.166	42.855	77.296	81.298	64.900	63.136	60.074	64.744
42	58.321	67.130	62.038	53.821	48.109	47.767	82.767	86.913	67.385	69.574	64.941	70.942
47	61.338	71.549	66.275	57.524	50.740	52.029	86.379	90.770	70.266	73.672	67.835	72.623
58	68.536	79.898	72.323	61.531	56.771	58.189	91.410	98.784	75.455	81.542	73.124	79.591
70	73.555	94.169	86.461	73.023	68.677	69.704	102.659	109.090	82.852	89.248	81.393	83.309
81	80.710	101.764	92.884	76.806	71.823	74.809	108.887	115.707	86.999	96.537	86.840	90.267
92	85.187	102.210	97.979	79.932	75.067	77.725	112.100	118.186	89.209	98.007	89.649	90.708
108	94.709	112.806	109.700	87.723	81.841	85.817	119.900	126.135	93.880	107.997	95.677	102.405
126	96.862	113.057	110.243	92.073	86.488	87.157	124.154	129.443	96.534	108.508	96.263	109.001
154	97.539	120.794	115.886	92.483	86.906	87.553	124.535	135.494	96.737	117.284	96.957	109.505

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